DYNAMICS OF A PENAEID SHRIMP POPULATION AND MANAGEMENT IMPLICATIONS

By Joseph H. Kutkuhn, *Fishery Biologist* (*Research*)
Bureau of Commercial Fisheries, Galveston, Tex.

ABSTRACT

In assessing present utilization of a stock of pink shrimp (Penaeidae) that supports an important commercial fishery in the eastern Gulf of Mexico, the interaction of population growth and mortality is critically analyzed. Estimates of the parameters involved were secured through a mark-recapture experiment wherein a biological stain served as the marking agent. The experiment was oriented in space and time so that exploitation of the marked population, which initially consisted of individuals uniform in size, provided measures of growth and mortality in the parent age group during and immediately following its transition from prerecruit to postrecruit status. Throughout the experiment, the entire stock as well as the marked population were heavily fished. Upon examining the question of whether or not the fishery's production could be improved by postponing the start of fishing until the shrimp reach a size greater than the 70 headless-count designation now generally viewed as a practicable minimum, it was noted that expected growth, although relatively high, would be insufficient to offset substantial losses due to expected natural mortality. Even with a moderate increase in growth rate, an appreciably reduced natural mortality would have to be indicated before such a move could be considered feasible. Maximum potential yield in both weight and value is obtained with the minimum acceptable size that the fishery currently imposes.

Broadly speaking, the basic goal of biological research undertaken by the Bureau of Commercial Fisheries is to gain the best possible understanding of how fishing and the principal environmental factors (once they are determined) govern the size of commercial fishery resources, and hence the yield of fish and fishery products. Its attainment would, theoretically, enable us to establish guidelines for maintaining any resource at about that level where production or, perhaps, economic advantage is highest. One should not gain the impression, however, that such a level can be held static over long periods of time, but recognize instead that it is subject to fluctuation from year to year in response to an everchanging environment and thereby presupposes continual readjustment of fishing intensity.

Utilization is associated very closely with the concept of resource maintenance. In the connotation of the phrase "conservation of natural resources," maintenance and utilization are, in fact, not mutually exclusive. But it is always likely that long before research can produce a scheme for effective resource maintenance, it will provide ad interim some indication of how a resource should be best utilized. Fishery research, which largely embraces the field of population ecology (including dynamics), becomes most efficient when it programs for short-term or intermediate as well as long-term objectives. It is noteworthy that the processes of achieving both types of objectives very often require the same basic data.

For nearly as long as Gulf of Mexico shrimp resources have been exploited, concern has prevailed as to whether they have always been utilized to best advantage. Many believe that the minimum size of commercially acceptable

shrimp should be increased, that the harvesting of any age group (or "brood") should be delayed until, by virtue of a high growth potential, maximum (or at least a greater) weight or biomass is reached. Phrased more simply, the question posed and heretofore not answered satisfactorily is: At what size per individual should an age group of shrimp begin to be harvested so as to realize the maximum yield from that group during its life span?

This question has important economic implications and requires that we understand the relationships between, and can measure, the rates of two concurrent biological processes: (1) *Growth*, the increase in shrimp size per individual per unit time, and (2) *mortality*, the numbers of shrimp dying per unit time (particularly due to natural causes).

Over the years, fishery biologists have found population growth and mortality parameters highly elusive. Recently, however, as part of its long-range shrimp research program, the Bureau of Commercial Fisheries perfected a very satisfactory process of marking shrimp that now permits such parameters to be approximated by the useful mark-recapture technique. The marking system proving so successful is the stain-injection method. Menzel (1955) is generally credited as having conceived its use on shrimp; Dawson (1957) as having substantiated its potential by means of laboratory experimentation; and Costello (1959, 1964) and Costello and Allen (1960) as having developed its large-scale application afield.

This paper first presents the results of a mark-recapture experiment with a rather well-defined stock of pink shrimp, *Penaeus duorarum* Burkenroad, which supports an important commercial fishery in southwest Florida, the widely known Tortugas fishery. After documenting the required estimates of growth and mortality, the paper then describes their synthesis through a theoretical yield equation to attempt an answer to the question stated earlier. In so doing, it draws in small part on the results of yet another mark-recapture experiment conducted with the same species, but for a different purpose, just prior to the one of primary interest.

Though it was classified as merely preliminary and expanded efforts were to be scheduled only if it achieved any reasonable degree of success, the Tortugas experiment proved successful well beyond our somewhat modest expectations. The quality of the resulting data is reflected in the kind of treatment they are given here. Such extensive treatment, regardless of the experiment's outcome, had not been anticipated in advance.

TORTUGAS MARK-RECAPTURE EXPERIMENT

DESCRIPTION AND REGULATION OF FISHERY

Lying west of Key West, Fla., reaching little beyond the 30-fathom contour, and extending not much farther northward than the 25th parallel, the Tortugas trawling grounds seasonally experience some of the most intense shrimp fishing seen in the Gulf of Mexico (fig. 1). Stimulating this activity is the appearance of large numbers of subadult pink shrimp which emerge in closely spaced surges from the shallow "nursery" grounds in Florida Bay to the east.[1] Although maturing shrimp may enter the fishing grounds at all seasons, it is in September-March that migrations are greatest and fishing is heaviest. Practically all fishing occurs at night when the pink shrimp is most active and hence most vulnerable. Like its close relative the brown shrimp, *P. aztecus* Ives, this species usually burrows and is therefore comparatively inaccessible during the hours of daylight.

Most trawlers operating on the Tortugas and adjacent grounds are of the characteristic Florida design (fig. 2). For all practical purposes they are nearly uniform in size and power, and employ fishing gear of roughly the same specifications (Iversen and Idyll, 1959; Kutkuhn, 1962).

The Tortugas fishery together with a lesser one, the Sanibel fishery, which is centered roughly 100 nautical miles to the north, did not become well established until the early 1950's (Idyll, 1957). A question often raised and now being examined is whether populations supporting both fisheries are genetically discrete, or whether they are continuous—even though continuity may prevail only at widely spaced life history stages. Evidence acquired to date tends to support the assumption made in this study that the Tortugas fishery largely depends on a stock of pink shrimp which is essentially separate from that sustaining the Sanibel fishery (Costello and Allen, 1960; 1961).

[1] Idyll (1957), Dobkin (1961), and Cummings (1961) should be consulted for a detailed account of pink shrimp life history.
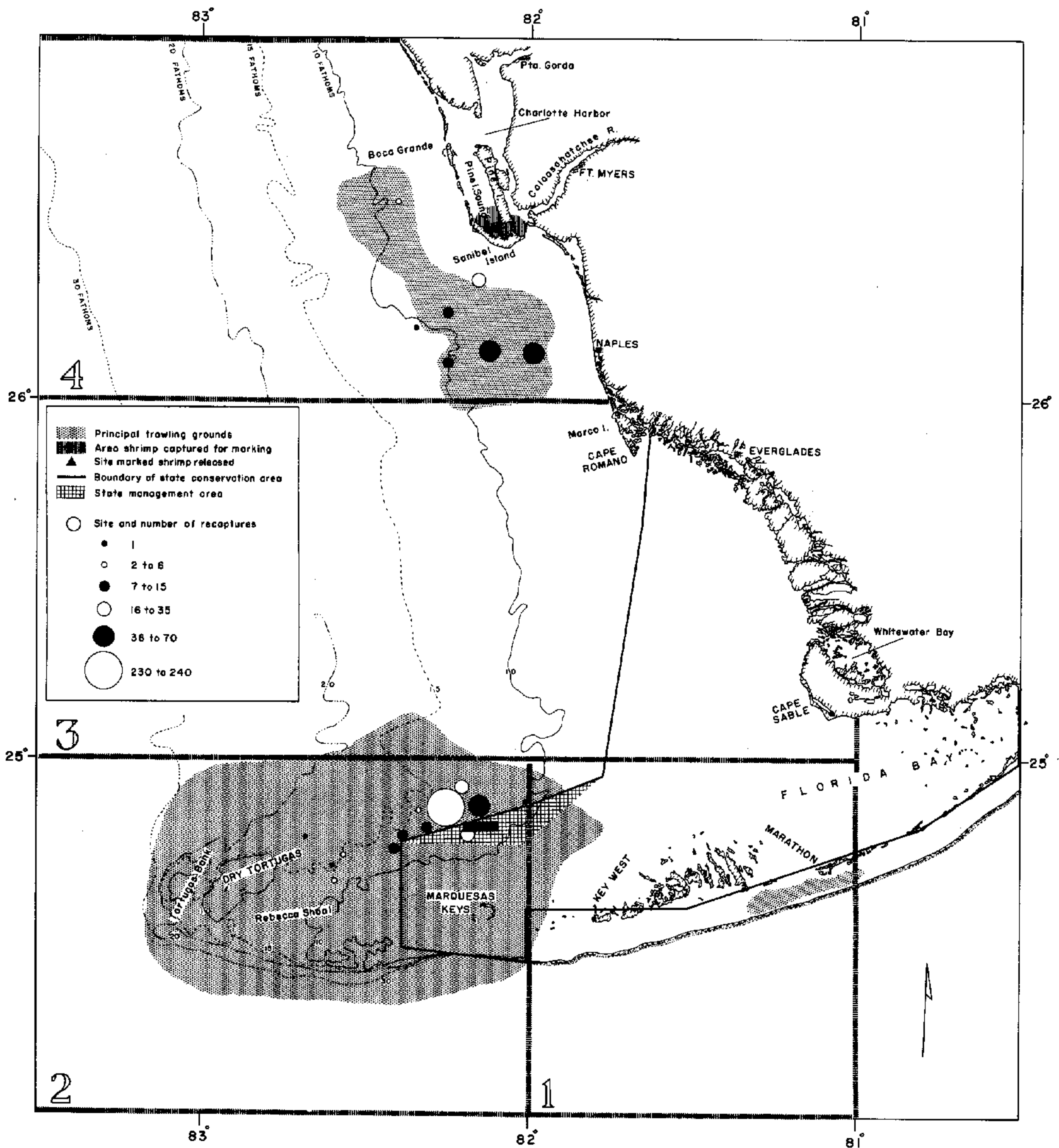
FIGURE 1.—General area in which mark-recapture experiments were conducted. Large numerals (1–4) identify coastal subareas employed in tabulating fishery statistics. Data shown in subarea 2 refer to the Tortugas experiment (September–December 1961), those in subarea 4 to the Sanibel experiment (December 1960–June 1961).

Annually contributing about 10 percent to the total Gulf production of shrimp, landings in the Tortugas fishery reached a peak of 23.6 million pounds in 1960, having risen from almost a record low of 12.9 million pounds the year before. The latter value represented a 44-percent drop from the previous high of 23.0 million pounds landed in 1958.[2] Since 1956 the fishery has seemingly had

[2] Source: Gulf coast shrimp data, published monthly by the Branch of Fishery Statistics, Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service.
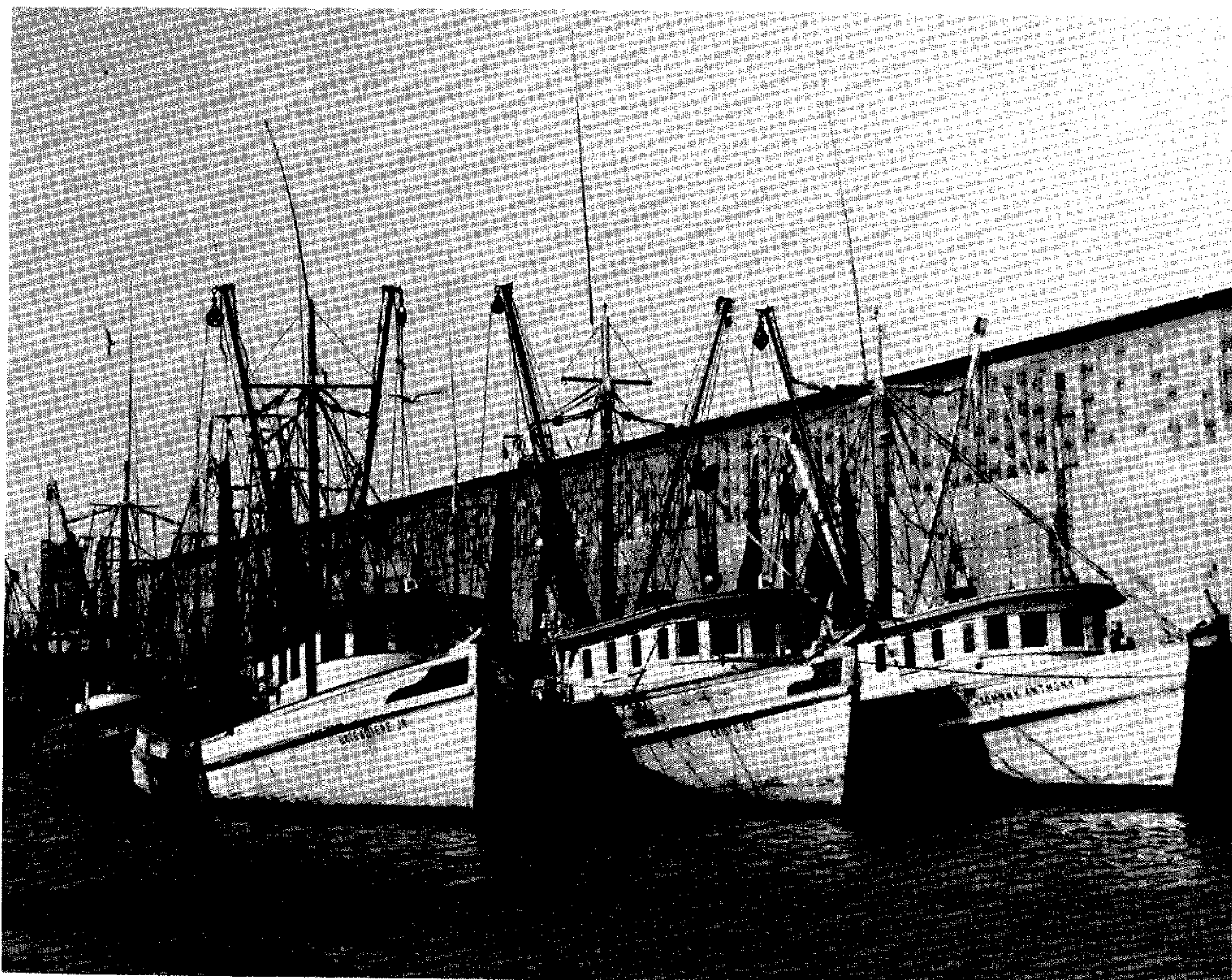
FIGURE 2.—Double-rigged, Florida-type trawlers predominate in the Gulf of Mexico shrimp fleet.

to rely to an increasing extent on small shrimp to keep production at a profitable level (Kutkuhn, 1962).

Believing that utilization might be improved by inhibiting the harvest of small shrimp, the Florida State Board of Conservation established in 1957 what is called a "control" area (Ingle, Eldred, Jones, and Hutton, 1959, figs. 1–3). This area was so situated that the preponderance of shrimp entering the open fishing grounds ostensibly migrated through it. Fishing was not to be permitted in the control area whenever periodic surveys disclosed that the shrimp therein were smaller than the size at which 50 headless and uniformly sized individuals weigh 1 pound. This regulatory concept was revised in mid-1961 when the Board delineated a permanently closed con-

servation area which incorporated part of the earlier control area and extended the latter's boundaries to enclose all of Florida Bay (fig. 1). Also circumscribed was a less extensive management (control) area from which only shrimp of 60 "headless-count" or larger may be taken.

MARKING PHASE

The Tortugas mark-recapture experiment was designed to take complete advantage of the physical and regulatory features of the fishery. Shrimp destined to make up the experimental population were to be captured, marked, and released just prior to the onset of heaviest expected fishing intensity. Concentrations of precommercial-size shrimp moving through the State management area offered the opportunity to

316

establish an experimental population from which could be obtained measures of growth and mortality in the parent population before and during as well as after its transition from prerecruit to postrecruit status.

Accordingly, operations using facilities provided by the Bureau's M/V *George M. Bowers* got underway on September 18, 1961, with the first releases of marked shrimp being made 2 days later. Shrimp were captured with small-mesh trawls hauled for very short intervals of time (frequently not more than 2 minutes) to minimize injury caused by compression in the net. To insure that only shrimp in prime condition entered the experiment, catches were held in tanks of circulating sea water for periods of at least 12 hours. After all weak and dying individuals had been removed, the remainder was sorted so that only those falling into a specified size range (total length) were retained for marking. This range was arbitrarily set using as a point of reference the modal length of available shrimp, such length having been determined by sampling catches made at the start of operations. Graded individuals were then marked by carefully injecting small quantities of a 0.25-percent aqueous solution of Trypan blue stain. Groups of marked shrimp were observed for at least 4 hours before being released, only the most vigorous individuals at the end of that time being selected for the experiment. These were released in lots of 100 at scattered sites and at irregularly spaced intervals during the marking period by means of a special release box (Costello, 1964). This device permitted the experimental shrimp to be returned directly to the bottom from whence they came (the depth being about 12 fathoms), and precluded large-scale losses due to predation by fishes and birds that would have occurred had the shrimp been released at the surface. Underwater movies taken during this operation reveal that marked shrimp released from the box immediately burrowed into the bottom, thereby satisfying the assumption that predation losses were, for all practical purposes, nonexistent. Because of judicious handling, selection, and release of the experimental material, it is hereinafter assumed that the total number of marked shrimp reintroduced into the parent population represented the actual or "effective" size of the marked population established during the marking period.

In the manner just described, an experimental population of 2,090 individuals was created within a 4-day period. Figure 1 shows the general location of capture and release sites. Measurements from an accumulation of small samples drawn each time a group of shrimp was released provided essential information concerning the population's length and weight attributes at the start of the experiment (table 1).

COMMERCIAL FISHING OPERATIONS DURING EXPERIMENT

Greatly influencing the outcome as well as the utility of results of experiments like the present one are the amount and distribution of recapture effort relative to the distribution of the experimental population. With all other potential sources of bias inoperative or satisfactorily accounted for, the rate at which marked individuals are recaptured becomes simply a function of the probability of recapture.[3] An index of this probability is, logically, the intensity of fishing or, in a rather restricted area such as is involved here, the fishing effort. A major problem is that the fishing effort often does not remain constant and thereby confounds the probability of recapture. It must be assumed at the outset, of course, that the experimental population soon reintermingles with and behaves in the same manner as the parent population (age group) from which it was temporarily removed.

Detailed information of fishing operations during the Tortugas experiment was provided by the Bureau of Commercial Fisheries Branch of Fishery Statistics which has agents stationed at major Gulf ports, including Key West, Fort

TABLE 1.—*Sex, length, and weight data from samples of the marked population at the beginning of the Tortugas experiment, middle of week ending Sept. 23, 1962*

[Number in marked population: 2,090. Estimated sex ratio: 60♂:40♀]

Sex	Number sampled	Carapace length [1]		Total length		Total weight	
		Mean	Range	Mean	Range	Mean	Range
		Mm.	*Mm.*	*Mm.*	*Mm.*	*G.*	*G.*
Male	168	19.2	17.9–20.1	90.1	84.2–94.1	5.9	4.8–6.8
Female	110	19.5	18.5–20.2	88.9	84.2–94.1	6.0	5.2–6.7
Total	278	19.3	17.9–20.2	89.6	84.2–94.1	5.9	4.8–6.8

[1] Carapace length is defined as the straight-line distance from the posteromost edge of the orbit to the posterior edge of the carapace where it intersects the middorsal line.

---

[3] Throughout this report, "recapture" refers to the marked shrimps' capture by the fishing gear; in contrast, "recovery" refers to their subsequent detection in commercial catches (or landings).

Myers, and Tampa, Fla. Estimates of the total effort expended weekly on the Tortugas grounds had to be projected from sample interviews (n) with trawler captains landing their catches at these ports. The procedure simply consisted of estimating from the sample data the average number of hours fished during each fishing trip and multiplying this by the total number of trips as determined by a canvass of processing plant records. Thus, the total hours fished in any week is given by

$$\hat{X} = N\bar{x} = \frac{N}{n} \sum_{1}^{n} x_i \qquad i = 1, 2, 3, \ldots n$$

where N is the total number of trips by individual trawlers to the fishing grounds, x_i is the number of trip-hours fished as reported by the captain of the ith vessel entering a weekly sample, and $\bar{x} = \dfrac{\sum_{1}^{n} x_i}{n}$ is the sample estimate of the mean number of hours actually spent fishing during each trip. The only difficulty arose when "uninterviewed" trips ($N-n$) extended over periods of more than 1 calendar week. In such cases, fractional trips for each of any 2 adjoining weeks had to be designated. These fractions were then summed together with trips contained entirely within respective weeks to obtain the weekly totals. Variances of the sample estimates were also calculated and, under the assumption of negligible or constant sampling bias, provided the estimates of total effort with an index of reliability. Hence

$$v(\bar{x}) = \frac{\sum_{1}^{n}(x_i - \bar{x})^2}{n(n-1)} \left(\frac{(N-n)}{N} \right)$$

and

confidence interval $(\hat{X})$: $\hat{X} \pm tN\sqrt{v(\bar{x})}$

where t is the value of the normal deviate corresponding to the desired confidence probability.

The Tortugas experiment lasted about 14 weeks; table 2 gives effort statistics and estimates, together with total landings, for each week plus the two that immediately preceded the start of the experiment. To provide some indication of how the effort was distributed on the fishing grounds, the weekly totals are also apportioned (on the basis of interview data) among three well-defined depth zones. Landing figures are not estimates but accumulations of actual catch weights obtained through a continuing canvass of all processing plants.

One other matter that will warrant consideration in a later section relates to the stage in age group development at which the member shrimps' commercial acceptance becomes complete, or selectivity no longer constitutes a factor. As employed here, the word "selectivity" does not refer to the selective properties of fishing gear but means, rather, the purposeful avoidance of shrimp of undesirable size even though they may be largely vulnerable to the gear in general use. Such selection is ordinarily accomplished by sorting catches or by test fishing for aggregations in which most individuals are of marketable size.

Unfortunately, the minimum marketable size of shrimp varies within the industry (or according to State law) from area to area around the Gulf, and in some localities may be only vaguely defined (or not stringently enforced). During the Tortugas experiment the fishery did not recognize a specific minimum size, with the result that sorting catches for the purpose of discarding small shrimp was not practiced. In fact, the only form of selection evident was the weekly expenditure of comparatively small amounts of fishing effort prior to the period in which the greater proportion of available shrimp reached a size of about 70 headless-count.

Examination of size (weight) frequency curves obtained from landings during the study period disclosed that selective fishing solely for medium and large shrimp was, practically speaking, inoperative (fig. 3). It suggested further that shrimp somewhat below the size designated herein as the minimum acceptable size (70 headless-count) were, if not entirely, almost wholly vulnerable and actively sought out by a sizeable though undetermined portion of the fishing fleet. Figure 3 clearly shows that small (in many instances, very small) shrimp predominated in Tortugas catches during the last 15 weeks of 1961. This fact lends credibility to the assumption that bias due to the selective action of the fishing gear was negligible and that the retrieval of marked shrimp of a size well below that tacitly set as a commercial minimum was almost entirely governed by the probability of a piece of gear encountering and capturing them, even though such probability

318

TABLE 2.—*Commercial shrimping operations in Gulf of Mexico statistical subareas 1–3 (Dry Tortugas-Marquesas) during September–December 1961*

Item	Week ending							
	9–9	9–16	9–23[1]	9–30	10–7	10–14	10–21	10–28
Total number of trips (N)	41	77	81	88	80	88	35	115
Number of trips sampled (n)	7	15	21	19	23	27	16	26
Mean number of hours fished per trip ($\bar{x}$)	28.8	35.8	26.0	31.8	49.7	32.1	26.2	32.9
Variance of mean $v(\bar{x})$	22.0	10.8	5.8	20.1	8.1	6.9	5.8	3.1
Coefficient of variation	0.16	0.09	0.09	0.14	0.06	0.08	0.09	0.05
Estimated total effort in hours ($\hat{X}$)[2]	1,180±250	2,760±330	2,110±250	2,800±510	3,980±290	2,820±300	920±110	3,780±270
—at: 0–10 fathoms								
11–20 fathoms	1,180	2,760	2,110	2,600	3,720	2.770	920	3,780
21–30 fathoms				200	260	50		
Percent of total effort in Subarea 3	1	1	1	9	5	7	3	10
Total landings[3]	42.1	287.9	301.6	212.2	227.3	179.9	72.8	411.8

Item	Week ending								
	11–4	11–11	11–18	11–25	12–2	12–9	12–16	12–23	12–30
Total number of trips (N)	97	206	270	177	175	201	217	161	67
Number of trips sampled (n)	20	62	97	69	37	53	74	48	2
Mean number of hours fished per trip ($\bar{x}$)	41.7	28.3	37.3	30.7	39.9	44.4	42.1	35.9	24.0
Variance of mean $v(\bar{x})$	12.1	3.2	3.2	3.7	10.0	6.3	3.0	3.3	23.3
Coefficient of variation	0.08	0.06	0.05	0.06	0.08	0.06	0.04	0.05	0.20
Estimated total effort in hours ($\hat{X}$)[2]	4,040±440	5,830±480	10,070±630	5,430±440	6,980±730	8,920±650	9,140±480	5,780±380	1,610±420
—at: 0–10 fathoms						180	330	80	390
11–20 fathoms	3,680	5,600	8,760	4,890	6,840	8,060	7,820	5,380	1,190
21–30 fathoms	360	230	1,310	540	140	680	990	320	
Percent of total effort in Subarea 3	5	3	6	9	1	6	4	8	1
Total landings[3]	365.3	680.2	763.7	215.8	240.1	467.3	433.1	189.9	39.0

[1] Week in which experiment began.
[2] 0.80 confidence intervals.
[3] Thousands of pounds (whole shrimp).

was represented in part by purposively selective effort. It follows that the likelihood of recaptures being subsequently recovered from commercial landings had to be presumed essentially constant throughout the experiment regardless of shrimp size.

RECOVERY PHASE

Extensive publicity coverage preceded and continued during the experiment. With the assistance of the Bureau's Branches of Fishery Statistics and Market News, cooperation in the retrieval of stained shrimp was solicited through correspondence, market reports, and personal interview from all industry segments as well as from State conservation agencies and the Gulf States Marine Fisheries Commission. The press, radio, and television provided additional coverage. A reward of $2 was offered for the return of any marked shrimp when accompanied by information regarding its place and date of capture. Posters to this effect (fig. 4) were conspicuously placed in all processing plants adjacent to the area in which the experiment took place. Close contact with fishermen and processors was maintained at all times.

Return of marked shrimp began immediately with 47 having been recovered before the end of the experiment's first week, referred to herein as the "period of release." Fortuitously, the State management area in which the marked shrimp were released (fig. 1) was opened to commercial fishing 2 days after the experiment got underway. In all, 443 or 21 percent of the total number liberated were eventually recaptured and returned for verification.[4] Daily distribution of recaptures is shown in figure 5. To facilitate subsequent analysis, they are grouped by calendar weeks (top of fig. 5).

Recovery continued strong for the first 8 weeks, reaching a peak during the sixth week and then dropping sharply (fig. 5). No marked shrimp were recovered after the 13th week. This abrupt attenuation reflected a real decline in the experimental population since associated recapture (fishing) effort did not decrease but rose significantly. Emigration of marked shrimp from the range of effective fishing effort appeared negligible (fig. 1), with no individuals being taken beyond 20 fathoms (only two outside 15 fathoms) or north of the 25th parallel despite measurable expenditures of effort at both locations (table 2). In general,

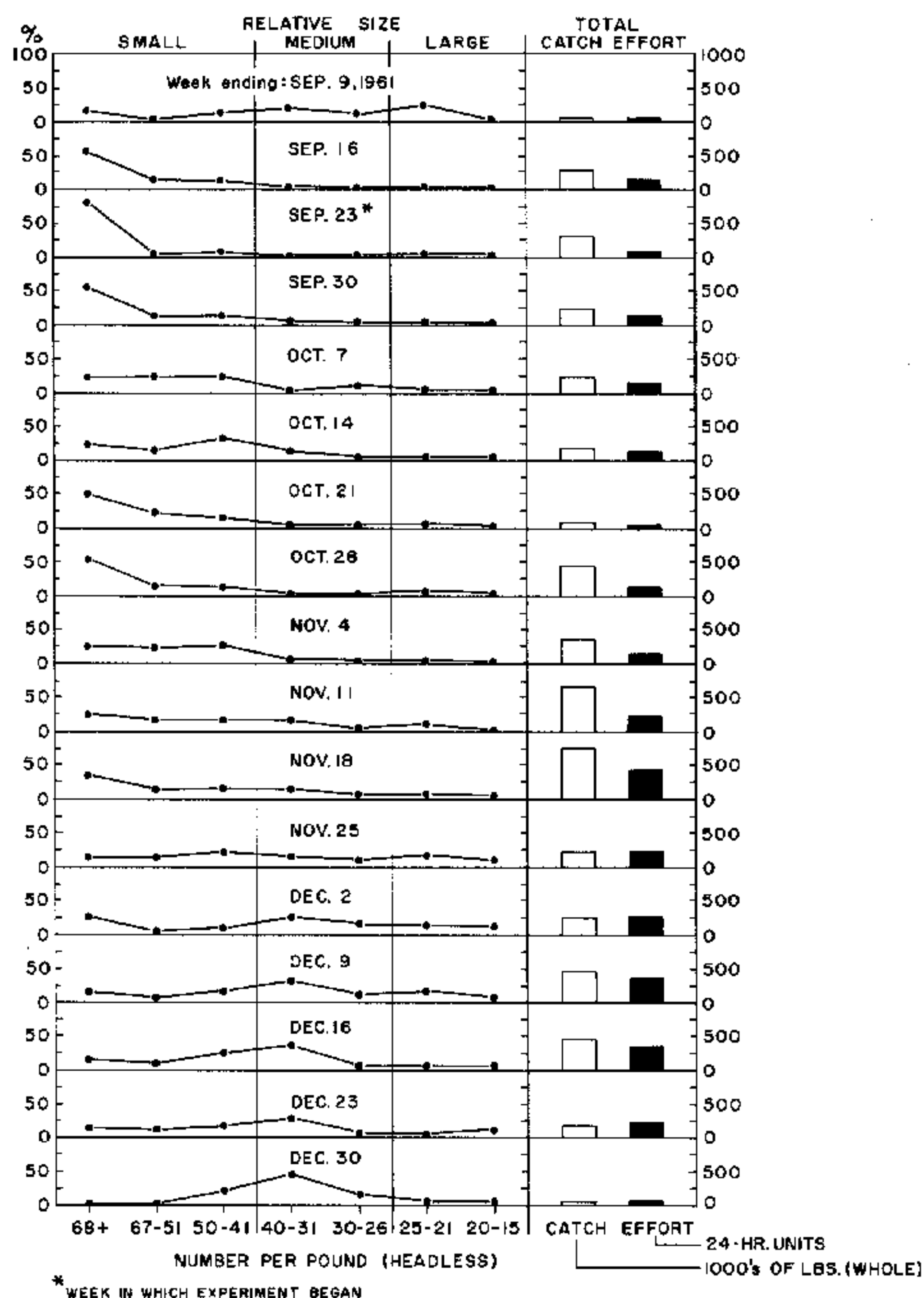[4] One marked shrimp returned 3 months after recapture was not included in subsequent analyses.

FIGURE 3.—Weekly commercial catch and effort statistics from the Tortugas pink shrimp fishery (statistical Subareas 1–3), September–December 1961.

what little movement was observed for the marked shrimp during the course of the experiment seemed to be in a west-northwesterly direction.   As will be shown later, the week in which most marked shrimp were recaptured (sixth week, October 22–28) coincided with that during which the preponderance of the experimental population attained the "minimum" commercial size designated earlier.   In other words, selective fishing by a heretofore undetermined portion of the fishing fleet ceased to be a factor at approximately this point.

Slightly less than three-fourths of the marked returns were detected while handling catches at sea.   Because of the consistently small size of shrimp taken during the experiment (fig. 3), the great majority of catches had to undergo complete processing ashore.   Such treatment entailed removing the head of each shrimp by hand, an

Shrimp have been marked with blue and green biological stains to obtain information on movements, growth, and rate of harvest. The color appears only on both sides of the head (in the gills) as shown in the illustration.

LOOK FOR COLOR HERE
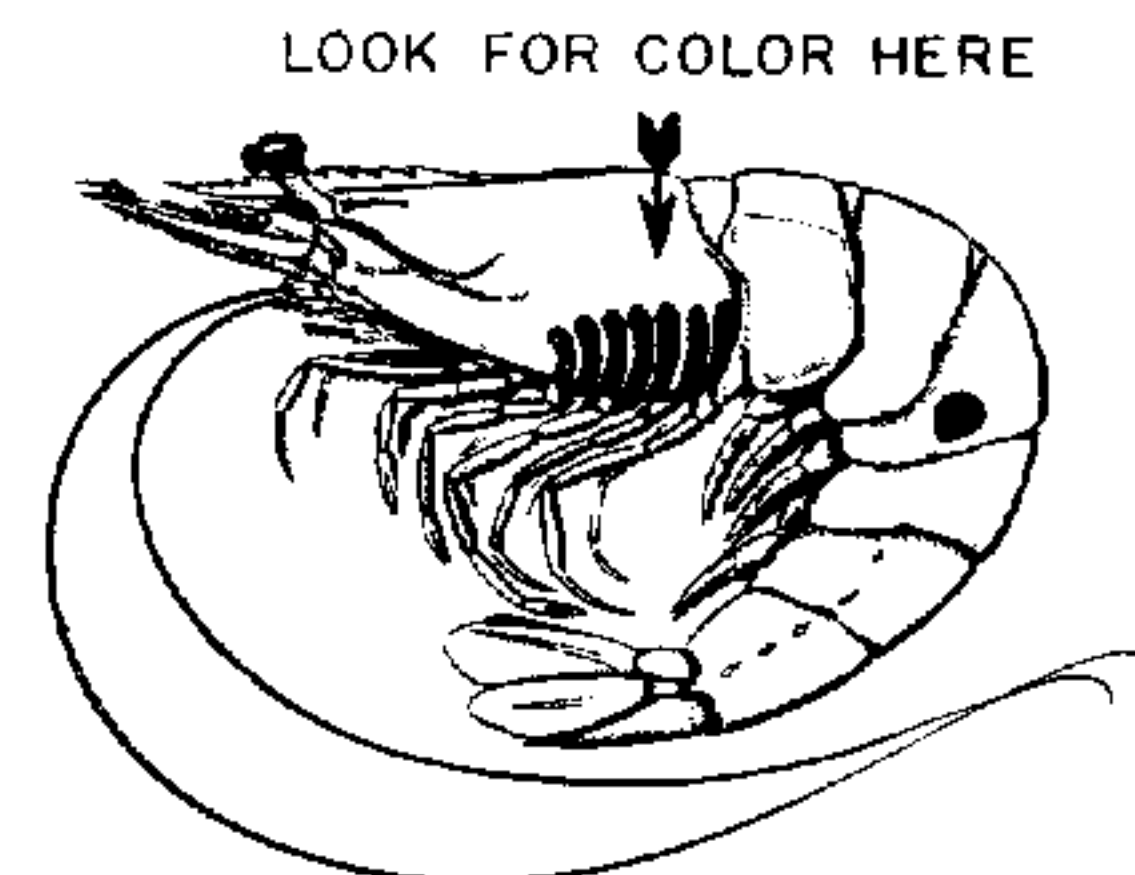
A reward of $2.00 will be paid for stained shrimp when returned with the following information:

1. Exact place the shrimp was caught.
2. Date the shrimp was caught.

Notify by mail the U.S. Fish and Wildlife Service, No. 1 Rickenbacker Causeway, Miami, Florida, or contact any Fish and Wildlife Service agent at port of landing. Please include name of vessel with the information submitted.

FIGURE 4.—Typical poster advertising reward for the return of marked shrimp.   Blue stain was employed in both the Tortugas and Sanibel experiments.

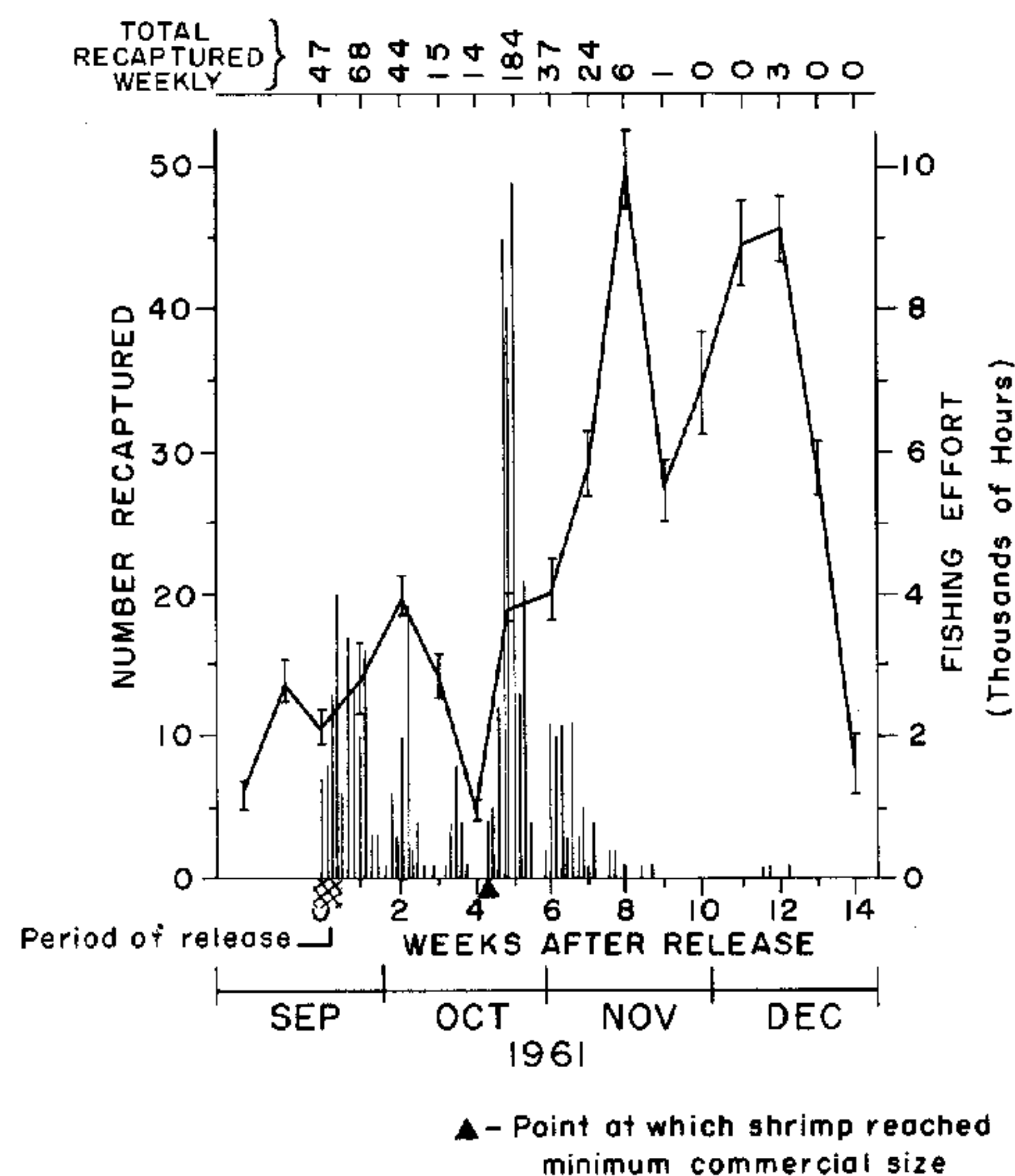▲ - Point at which shrimp reached minimum commercial size

FIGURE 5.—Temporal distribution of fishing effort and of marked shrimp recaptured during the Tortugas experiment.   Vertical bars from the abscissa represent number recaptured on indicated days.   Vertical lines through points on effort curve define 0.80 confidence intervals for weekly effort estimates.

operation usually undertaken aboard the fishing vessel when most of the catch consists of medium-size or larger shrimp. Regardless of where beheading takes place, however, the chances of detecting marked specimens in the process are always very good to excellent. Under the conditions prevailing in most processing plants they are highest. All recovered shrimp not found at sea by vessel crews were later retrieved by plant personnel.

So far as is known, only a small fraction of all landings made within the study period escaped such close scrutiny, this occurring when landings infrequently had to be shipped directly to canneries located on the northern Gulf coast.

SANIBEL MARK-RECAPTURE EXPERIMENT

Though specifically designed for another purpose, the Sanibel experiment yielded growth data that proved useful in corroborating comparable data derived from the Tortugas experiment. By way of providing a brief description, the former experiment began about 9 months before the latter and extended over the period December 1960 to June 1961. In an attempt to determine the migration patterns of juvenile pink shrimp as they leave estuaries in the vicinity of Sanibel Island, Fla., 32,900 shrimp were marked with Trypan blue stain and released in Pine Island Sound. Commercial fishermen subsequently recaptured 155 (or 0.5 percent) at the locations indicated in figure 1.

Individuals making up the experimental population were first graded to uniform size though not nearly so carefully as those selected for the Tortugas experiment. A sample of 463 specimens taken at the experiment's start revealed a mean total length and corresponding weight of 75.3 mm. and 3.5 g., respectively. Sexes occurred in the estimated ratio of 46 males to 54 females.

ESTIMATION OF GROWTH

METRIC CONVERSIONS

Solution of the yield equation employed in a later section postulates that the average growth of each individual making up the population of interest be expressible in terms of weight, and that

the average relationship between an individual's weight and length be firmly established.

Since it is ordinarily impractical to measure precisely in the field the weight of animals as small as shrimp, sampled individuals for the most part must be measured as to length at the sampling site, or preserved (rarely frozen) and later measured, again according to some length criterion, at a more convenient time and place. Subsequently required in either case are appropriate means for converting length to weight units.

Three situations that are met in the course of studies like the present one, and in shrimp research generally, may thus be defined. The first entails reciprocal conversion of the linear size indices commonly used in shrimp work, viz, total and carapace length. In this study, for example, total length was the criterion used to grade shrimp selected for the Tortugas experiment. But the sample from which the actual size-range limits were determined had to be preserved (formalin) for later measurement under more favorable conditions. Since the total length of shrimp so treated cannot be accurately measured because of the distorting and hardening effects of the preservative, carapace length, which remains unimpaired, provides the most practicable index of shrimp size. The statistical relationship between total length and carapace length serves to transform either linear dimension to the other and proves particularly useful when comparing the results of research in which the methods of measurement differ from one study to the next.

The two remaining situations prevail where interest centers on the transformation of linear to weight units, i.e., (1) from total length to total weight when length measurements can be made at the time of sampling and (2) from carapace length to total weight when the sample material must first be preserved.

Over the period August 1960 to January 1961, and independent of the experiments reported herein, weight and corresponding length measurements were obtained from slightly more than 1,600 pink shrimp sampled from commercial catches taken along the east and southwest Florida coast (Biscayne Bay and the Tortugas-Marquesas area, respectively). An indication of their statistical strength in terms of sample distribution by sex and relative size is given in table 3.

TOTAL LENGTH-CARAPACE LENGTH RELATIONSHIP

A plot of the mean carapace lengths for each of 28 male and 36 female, 5-mm. total-length classes suggested that the relationship between the two attributes could be best described by a simple exponential (fig. 6). Up to a total length of about 150 mm. the relationship for both sexes appears nearly identical and is, for all practical purposes, rectilinear. Beyond this length, however, defini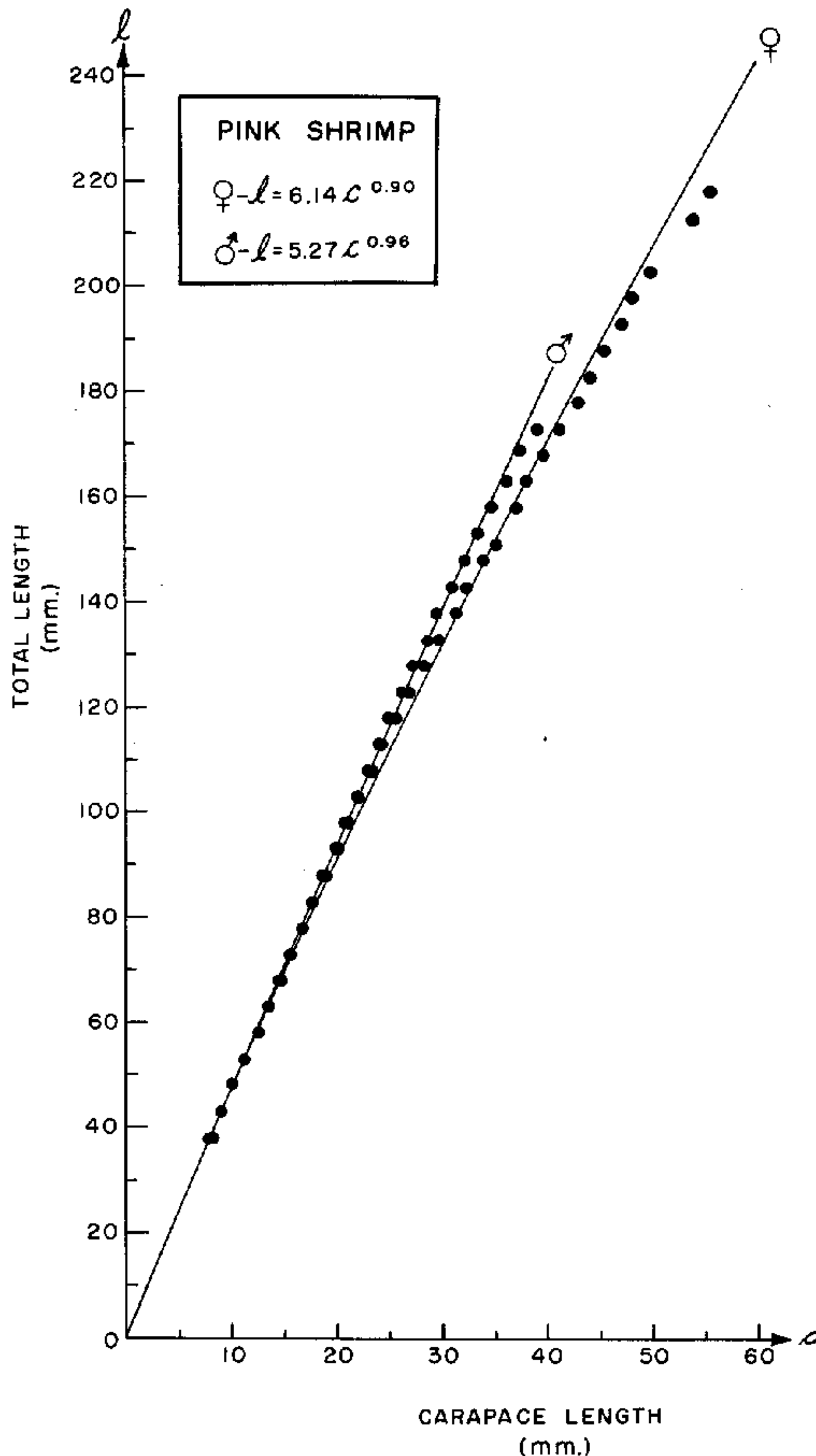te curvature indicates that increases in carapace length (c) do not keep pace with increases in total length (l). Note also in the larger shrimp a marked sex differential in the total length-carapace length ratio. Thus, for shrimp of the same total length, females will have a greater carapace length than males, the difference increasing with size.

TABLE 3.—*Distribution by sex and relative size of pink shrimp sampled during 1960–61 in south Florida for weight and length measurements*

Sex	Number of specimens measured	Range in total length	Number of 5-mm. length classes	Average number of specimens per class	Number of classes with less than 15 specimens
		Mm.			
Male	729	35–175	28	25	3
Female	888	35–215	36	26	3
Total	1,617	35–215	36	45	3

For pink shrimp not exceeding 170 mm. total length (equivalent to 16 headless-count), the information provided in figure 6 will permit, graphically or mathematically, reasonably accurate estimation of total length from a known carapace length. Although precision diminishes somewhat above this limit, resulting estimates will still be sufficient for most purposes.

Linear conversions indicated in table 1 and elsewhere in this study employed the information given in figure 6.

Weight-Length Relationships

Plots of data categorized as above showed weight to be a simple power function of length. Either the fitted curves or equations for total weight (w) as a function of carapace length (fig. 7), and as a function of total length (fig. 8) may be used to estimate weight from either linear dimension with reasonable precision and accuracy. Close examination revealed some seasonal variation in the relationships, but not enough to be of practical significance. Sex differences are clearly evident in each case with the disparity being particularly prominent in the total weight-carapace length ratios. Among shrimp having the same carapace length, males, on the average, not only possess a greater total length but are heavier than females. It follows, conversely, that in individuals of the same total length, the males will weigh less than the females and have a shorter carapace. These differences should be borne in mind whenever metric conver-

PINK SHRIMP

$♀-l = 6.14\,c^{0.90}$

$♂-l = 5.27\,c^{0.96}$

FIGURE 6.—Total length-carapace length relationship in pink shrimp.
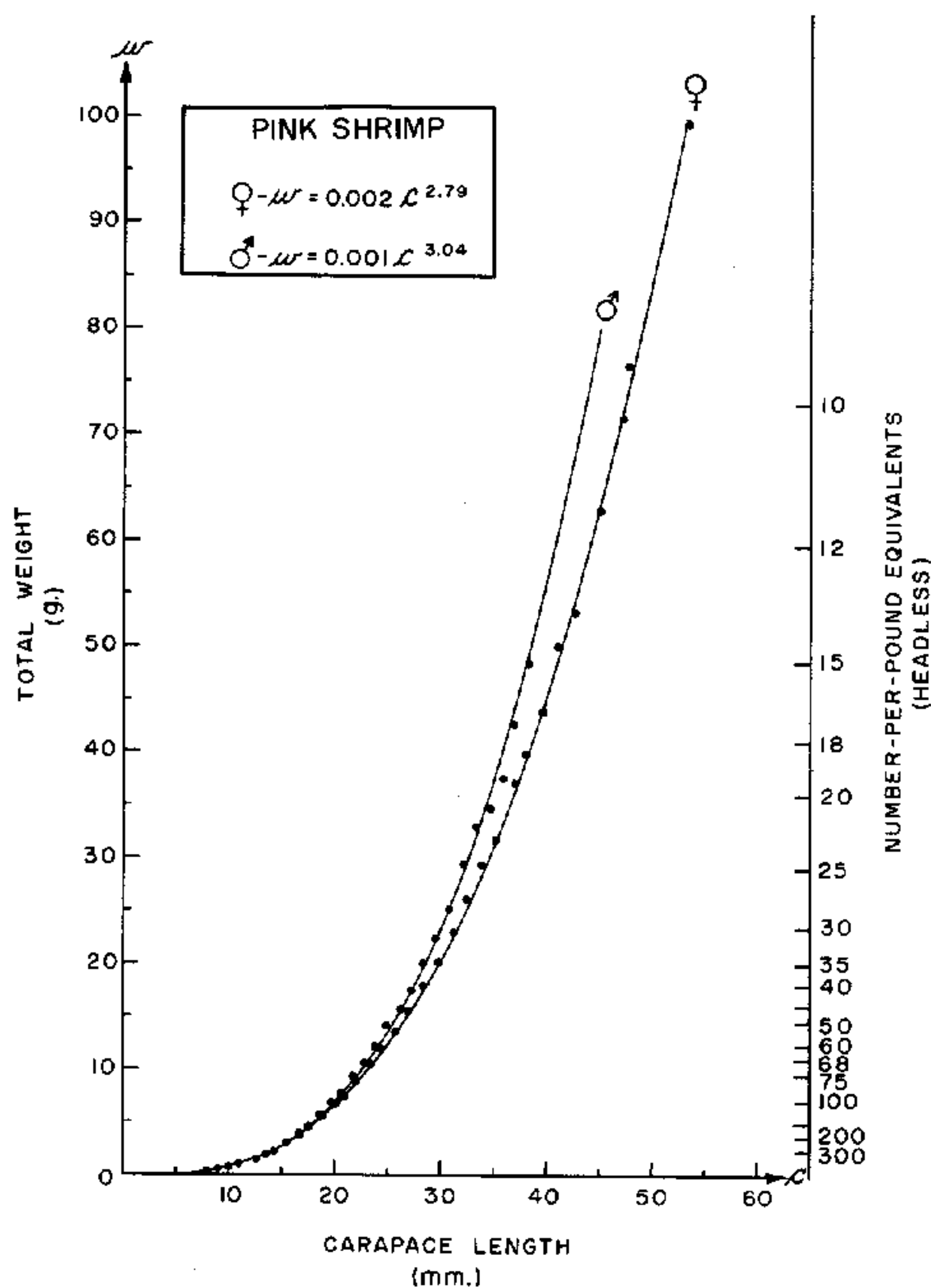
FIGURE 7.—Total weight-carapace length relationship in pink shrimp.

sions of the types treated here become necessary.

All length-to-weight conversions required in subsequent analyses are made with the information shown in figures 7 and 8.

Of particular interest in the present study is whether or not shrimp growth is isometric or, more specifically, whether or not the total weight-total length relationships derived above conform to the well-known cube law, viz, $w=al^b$, where $b=3$. Conformation (or lack thereof) should be acknowledged when growth and mortality parameters are integrated to solve the yield equation referred to earlier and described in a later section. The fact that the parameters of the mathematical expressions relating total weight to total length proved almost identical for both sexes (fig. 8) simplified somewhat their statistical assessment. Upon being tested with sexes separate or combined, the hypothesis of no exponents differing significantly from $b=3$ had to be rejected. [For sexes combined—$H_0: b=3.00$ when in fact $b=3.14$—$t=$

11.16, compared with $t_{.05}$ (33 degrees of freedom) = 2.04.]

ESTIMATING GROWTH PARAMETERS AND FITTING CURVES

Recaptures from the Tortugas experimental population provided some of the best data yet obtained for describing growth in North American Penaeidae (table 4). In synthesizing these data for practical application later, a growth differential between sexes materialized as the only real impediment, there being no evidence of growth inhibition by the mark employed. Ideally, growth constants for both sexes should be treated separately (via summation methods) in all yield predictions, particularly since the maximum size attained by male shrimp appears to fall far short of that attained by females (re table 3). Whether or not both sexes have equivalent life expectancies poses still another argument that would have to be reconciled. But, to obviate undue complexity and because breakdown of recapture data by sex
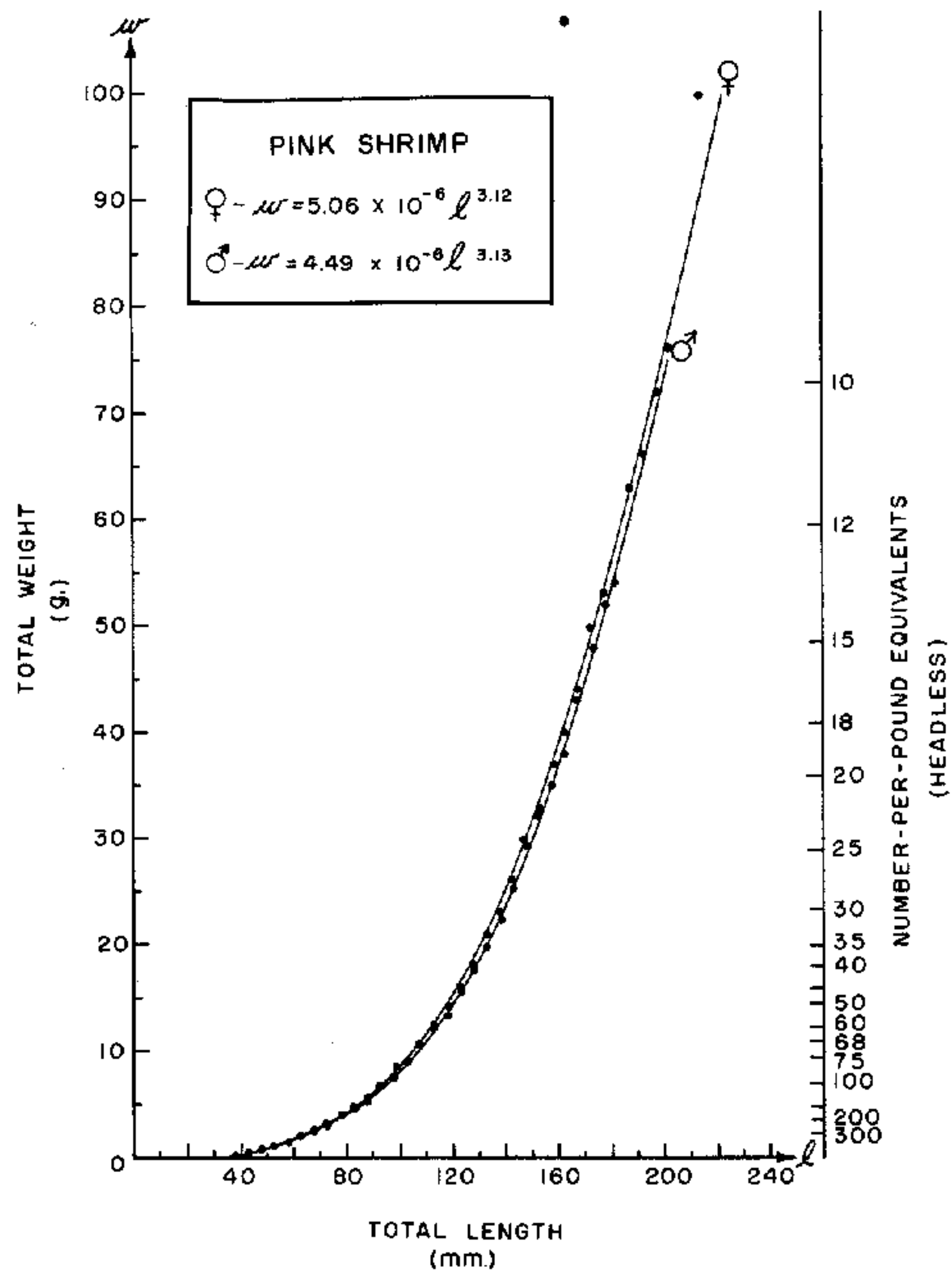

FIGURE 8.—Total weight-total length relationship in pink shrimp.

would have resulted in diminished reliability of sample length and weight estimates, each growth statistic hereinafter computed and substituted in yield equations reflects a compromise or "sexes-combined" situation. Although such statistics are in a sense artificial, their use is justified in that they define the average growth pattern within the experimental population during that period when the age group represented was enjoying greatest biomass, was most accessible, and its sex ratio had not yet begun to indicate a preponderance of females. Each estimate obtained may be viewed as lying intermediate between some upper value for females and a lower value for males.

It follows also that experimental length and weight data from a sexually heterogeneous population yield the most reliable growth-parameter estimates when the sex ratio of marked recaptures remains constant throughout the experiment. In the case of the Tortugas experiment, the sampling distribution of ratios generated over the period $t_1 - t_8$ revealed no significant statistical departure when checked for goodness of fit against the uniform distribution theorized from the sex ratio established at the experiment's beginning [$x^2 = 12.15$ compared with $x^2_{.05}$ (6 degrees of freedom) $= 12.59$].

TABLE 4.—*Mean lengths and weights of marked pink shrimp recaptured during successive weeks of the Tortugas experiment, September–December 1961 (sexes combined)*

Week of experiment t_i	Number recaptured [1] n	Distribution of males	Mean total length l	Mean weight w	Range in weight	Equivalent number per pound (headless)
		Percent	Mm.	G.	G.	
0	[2] 325	60	88.8	5.9	4.9– 6.6	123
1	68	51	90.0	6.1	4.9– 7.1	119
2	39	54	92.5	6.6	5.5– 8.3	110
3	15	47	103.9	9.5	8.0–10.2	76
4	11	61	106.0	10.2	8.1–11.3	71
5	176	55	109.8	11.4	7.5–15.8	64
6	35	42	113.1	12.5	10.1–18.3	58
7	22	67	118.7	14.5	9.6–17.6	50
8	6	67	123.2	16.2	13.4–19.2	45
9	[3] 1	100	123.4	16.4		44
10	0					
11	0					
12	[4] 2	50	130.4	19.5	18.7–20.2	37

[1] Total number of recaptures used for growth computation (422) does not agree with total number recaptured during experiment (442) because breakage or other damage precluded carapace-length measurement in some (20) specimens.

[2] Data from 47 recaptures combined with sample data (table 1) secured during period of release.

[3] Measurements from this specimen excluded from growth computation.

[4] One other specimen (♀) returned 3 months after recapture was not included in analysis.

Although comparable growth data contributed by the Sanibel experiment did not meet the requirement of constant sex ratio (table 5), their greater temporal range gave a better indication

of the probable shape of the pink shrimp growth curve. Subsequent plots of mean weights of marked shrimp recaptured during successive time increments within each experiment suggested that von Bertalanffy's (1938) growth-in-weight equation offered, as it has in a wide variety of species, the most meaningful and at the same time the most practical solution to the problem of mathematically characterizing shrimp growth (fig. 9). In addition to the exponent b, which is obtained from the weight-length relationship, the function itself,

$$w_t = W_\infty (1 - e^{-K(t - t'_0)})^b,$$

contains three parameters that are presumed effectively constant when describing growth over the greater part of the shrimp's life span. W_∞ represents the asymptotic or maximum weight attained by the average shrimp; K is a coefficient proportional to the rate of catabolism; and t'_0 defines a hypothetical age at which the shrimp's weight would have been zero had its growth pattern always been the same as that suggested by the experimental data.[5] If growth be assumed isometric, then b takes the value 3; in the present case, the estimated value, 3.14, was employed. For more extensive discussions on the rationale underlying the von Bertalanffy equation and the advantages that render it particularly adaptable

TABLE 5.—*Mean lengths and weights of marked pink shrimp recaptured during successive 4-week periods of the Sanibel experiment, December 1960–June 1961 (sexes combined)*

Month of experiment t_i	Number recaptured n	Distribution of males	Mean length l	Mean weight w	Range in weight	Equivalent number per pound (headless)
		Percent	Mm.	G.	G.	
0	[1] 463	46	75.3	3.5	1.8– 8.9	207
1	[2] 1	0	111.7	12.1		59
2	4	100	109.1	11.0	8.2–13.8	66
3	39	38	117.5	14.1	7.1–24.8	52
4	65	52	123.0	16.3	8.1–29.5	44
5	38	39	136.1	22.5	14.4–40.2	32
6	6	33	145.8	27.7	21.9–32.5	26
7	[2] 1	0	157.5	35.2		21

[1] Indicates number of specimens sampled to determine mean length and weight of marked shrimp at start of experiment.

[2] Data from single recaptures not used in growth computation. One additional specimen (♂) recaptured in 12th month was also disregarded.

[5] To remind the reader that the estimation of growth parameters from mark-recapture experiments necessarily involves the translocation of size and time axes, the notation t'_0 herein replaces the standard t_0. The latter represents the true population parameter which may be most accurately estimated only when a reasonably complete series of weight-at-age data for a given species is available. For all practical purposes, it is assumed that the difference between t'_0 and t_0, or bias, is negligible.

Throughout this paper, the symbols e and ln designate, respectively, the base of, and abbreviation for, the natural or Naperian logarithm.
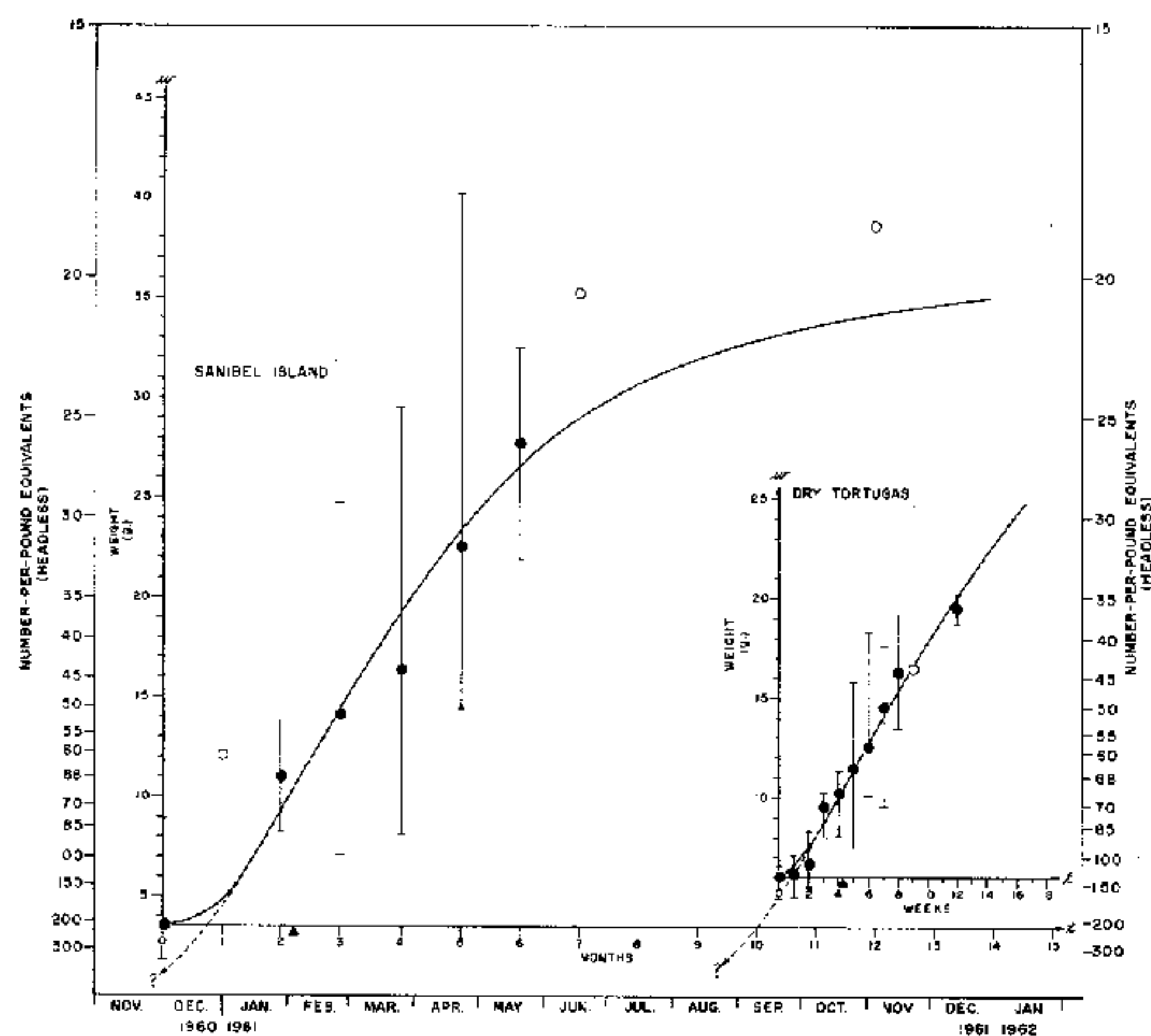
FIGURE 9.—Growth in weight of pink shrimp. Curves are fitted to mean weights of marked shrimp recaptured during successive time intervals of the Tortugas and Sanibel experiments (sexes combined). [Open circles indicate weights of single recaptures not used to fit curves.]

to incorporation in theoretical population models, the reader is referred to the works of von Bertalanffy (1957), Beverton and Holt (1957), Ricker (1958), and Tomlinson and Abramson (1961).

Approximations to W_∞ were obtained by first transforming the von Bertalanffy equation to a form linear in $w_t^{1/b}$ and then fitting the linear regression of $w_{t+1}^{1/b}$ on $w_t^{1/b}$. The intersection of the resulting line with that of proportionality yielded, upon retransformation, the desired estimates (Beverton and Holt, 1957, p. 283). In effect, the intersect signifies the approximate weight at which the ratio of successive growth increments reaches unity, i.e., growth is arrested and maximum weight is attained. The slope of the regression line provides an estimate of e^{-K}.

A distinct disadvantage of this method when working with data from mark-recapture experiments is the requirement that weights be obtained for every one of a reasonably wide range of successive, equal-width time intervals. Unfortunately, W_∞ is quite sensitive to changes in the slope of the fitted line and therefore has real meaning only when the marked population that yielded the data was at all times completely vulnerable to the sampling (fishing) gear, the sex

ratio of recaptures remained static, and the resulting mean sample weights display consistent as well as good reliability. Thus, its estimation from the somewhat inadequate Sanibel data had to rely on but four pairs of values (from t_2-t_6), whereas that from the superior Tortugas data was substantiated by seven pairs (from t_1-t_8). Because of considerably less variation about the fitted line, the estimate derived from the Tortugas data is regarded the more stable, and hence the more meaningful of the two (table 6). When estimating W_∞, there was no suggestion in the case of the Tortugas data, and only faint evidence in the Sanibel data, that the fishing gear in general use was selective for faster-growing individuals during the early stages of either experiment.

TABLE 6.—*Pink shrimp growth statistics computed from mean weights of marked shrimp recaptured during successive time intervals of the Tortugas and Sanibel experiments (sexes combined)*

Experiment	Season	Duration	Width of experimental time interval, t	W_∞	K	t_0
		Weeks	*Weeks*	*G.*		*Weeks*
Tortugas	Sept.–Dec.	12	1	[1] 42.0	0.071	0.68
Sanibel	Dec.–June	32	4	35.6	0.339	3.20

[1] Equivalent to a size of 17 headless-count.

After adjusting w_t and W_∞ to unity at the beginning (t_0) of each series of data, the slope of the linear relationship

$$\ln\,(W_\infty^{1/b}-w_t^{1/b})=\{\ln\,(W_\infty^{1/b})+Kt_0'\}-Kt$$

provided estimates of K, and the ordinate at which the regression line intersects $\ln W_\infty^{1/b}$ gave estimates of t_0' (table 6). Substituting these in the von Bertalanffy equation, theoretical values for w_t were calculated and ultimately defined the curves depicted in figure 9. It is assumed that the values for the constant t_0', although based on data of weight at undetermined age, would have compared reasonably well with those obtained had the actual (rather than the relative) age at each t_t been known.

From table 6 and figure 9, it may be concluded that the results of both experiments are in large degree mutually corroborative. With the Tortugas results arbitrarily established (on statistical grounds) as the standard for comparison, W_∞ is of the same relative order of magnitude while the

growth indices, K, agree surprisingly well (comparative K from the Sanibel experiment $= 0.339/4 = 0.085$). Weekly growth during the Tortugas experiment averaged roughly 1.5 g. in terms of weight and about 3.4 mm. in terms of total length. From a commercial fisherman's viewpoint, the experimental data (table 4) reveal that it took 12 weeks for the average shrimp to increase in size from 123 to 37 count (headless). Observe also that the minimum commercial size (70 headless-count) in the marked populations was attained about 9 weeks following the start of the Sanibel experiment, and 4½ weeks after the Tortugas experiment began.

AGE AT RECRUITMENT—MAXIMUM AGE

If, as Beverton and Holt (1957) argue, biological rather than mere empirical significance be attached to von Bertalanffy's equation and, further, if the growth pattern as fixed by the constants computed earlier be assumed reasonably typical of pre- as well as postrecruit development, then extrapolation of the curves in figure 9 to the left of t_0 should provide a rough index to the actual ("average") age of shrimp making up each experimental population at the time it was established. Adding this to the time lapsing between an experiment's initiation and the attainment of minimum commercial size by its elements gives a measure of age at recruitment. Fear that the von Bertalanffy equation may not adequately describe growth during the shrimp's earliest developmental stages should not deter pursuit of such an index. No better approach to solving the vexatious problem of age determination in commercial Penaeidae has yet been developed.

In treating accordingly the results of the Tortugas experiment (upon which all subsequent analyses and discussions will be based), a value between 10 and 11 weeks was indicated as the probable age of shrimp released at the experiment's start. When this value is extended by the 4½ weeks the marked shrimp required to reach minimum commercial size, an approximation of 15 weeks for their age at recruitment is obtained. Despite the likelihood that this value may not be too precise, its order of magnitude is quite reasonable in view of what has been observed in a species closely related to (and often occurring with) the pink shrimp, viz., the brown shrimp.

Along the Texas-Louisiana Gulf coast and with little year-to-year variation in chronology, heightened spawning activity in offshore brown shrimp populations during February and March normally results in large masses of postlarvae entering adjacent estuaries during mid-March to mid-April. Present studies by personnel at the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Tex., are yielding good evidence that brown shrimp postlarvae, 8 to 12 mm. long when they reach the barrier island passes, are on the order of 3 to 4 weeks old.[6] Once in inshore waters they grow very rapidly and begin their seaward migration about mid-June as subadults of a size just below the 70-count minimum established above. Thus, the total lapse in time between hatching and attainment of 70-count size (about 10.5 g.) is roughly 15 weeks, which agrees very well with the value obtained for pink shrimp from the Tortugas experiment.

One other growth-associated feature of pink shrimp life history about which the yield equation employed in a later section requires information is the maximum age, on the average, that this species attains. For the common Penaeidae, it has been generally assumed on empirical grounds that 18 months (78 weeks) is a good approximation thereto (Kutkuhn, 1962). Recent analyses of weight frequency distributions in commercial pink shrimp landings indicate, however, that the lapse between an age group's recruitment and its disappearance from the fishery (i.e., its fishable life span) averages about 68 weeks (Kutkuhn, 1962). Hence, upon combining this value with that of the species' average age at recruitment calculated above, a value of 83 weeks, believed to be a better estimate of maximum age, is obtained.

ESTIMATION OF MORTALITY

BASIC ASSUMPTIONS

Computationally as well as conceptually, measurement of mortality—especially natural mortality—is without question more intractable than that of growth and therefore makes greater demands on experimental data. Moreover, since the investigator cannot guarantee that the results

---

[6] Lindner and Anderson (1956) offer supporting documentation in their study of the contemporary white shrimp, *P. setiferus*, whose postlarvae are also estimated to be about the same age when they enter estuaries at comparable sizes.

of even the most carefully executed mark-recapture experiment will satisfy all theoretical requirements, he is forced when attempting such measurement to rely heavily upon certain conditional assumptions that may or may not be warranted.

Potential sources of bias affecting the accuracy of mortality estimates anticipated from data yielded by the Tortugas experiment have already been discussed. To reiterate, assumptions for which reasonable substantiation was given are: (1) No, or only negligible, losses of experimental shrimp due to rough treatment at release, or to predation during and immediately after release; (2) no losses attributable at any time to after-effects of the mark (dye); (3) little if any movement of marked shrimp from the range of effective fishing during the experiment; and (4) negligible loss of recaptured shrimp because of failure to report them. Information indicating the percentage loss due to nondetection was not obtained, but the manner in which commercial catches were processed leaves little doubt that the likelihood of detecting marked shrimp was high (as was the incentive to do so). Nevertheless, a necessary assumption is that not only was the number of recaptured but undetected shrimp low, but that the ratio of undetected to detected recaptures did not change during the experiment.

THEORY AND EXPERIMENTAL RESULTS

All present-day theory constituting the framework of what is commonly termed "population dynamics" has as its point of departure the concept that the average rate of decline in any population (fish, shellfish, etc.) is at every instant proportional to population size. This relationship may be simply expressed by the differential equation

$$\frac{dN}{dt} = -ZN$$

which, upon integration, gives the geometric progression

$$N_t = N_0 e^{-zt} \tag{1}$$

with common ratio e^{-z}, N_0 the initial population size, and N_t the number in the population during any of a series of equal-width time intervals t. Two parameters, N_0 and Z, characterize the expression, with the coefficient Z referred to as the instantaneous rate of total mortality.

The foregoing theorem proves particularly useful in mark-recapture work since the initial size of a marked population, N_0, is almost always known. In some situations this feature readily permits the separation of Z into its components, viz., (1) mortality in the experimental population due to recapture (fishing), and (2) losses of marked members due to all other causes. These quantities are symbolized in the following analysis by the notation F and X, respectively (Beverton and Holt, 1957). Of major interest is the coefficient X, part of which represents true natural mortality, hereinafter denoted by the symbol M. Depending on the acceptability of assumptions concerning the degree to which marked members are not prone to loss other than through fishing and natural mortality, X itself can provide a reasonable approximation of M.

As revealed earlier (fig. 5), the probability of a marked shrimp being recaptured varied widely during the Tortugas experiment. It follows that the corresponding fishing mortality fluctuated accordingly, and that the effects of nonuniform recapture effort would therefore have to be eliminated before attempting to measure total mortality, Z, and, ultimately, natural mortality, M. Two approaches to the satisfactory measurement of Z with recapture data generated under such circumstances are employed herein, whereas only a single alternative offered itself as a solution to the more difficult problem of estimating X (i.e., M).

The first of the two methods used to determine Z entailed application of an analytical method developed for the simple situation where fishing effort (or intensity) does not change appreciably during an experiment. Its use here initially required that, rather than assume within each equal-width time interval a fixed but, between intervals, a successively different (i.e., a discontinuous) fishing mortality, the number of recaptures accumulating in every time interval be adjusted to a continuously uniform fishing effort throughout the experiment (table 7). Such an approach clearly infers that had a static fishing effort prevailed, the pattern of population decline expressed by theorem (1)—with all bias constant or negligible— would have been reflected. In other words, removing the confounding effects of a varying fishing effort served to eliminate all but that part of the overall recapture probability that would

have diminished predictably as the experimental population declined. It is noteworthy that adjustment of each value in the recapture time-series under discussion here was itself independent of time, and hence did not superimpose additional bias whose presence might further curtail the usefulness of mortality coefficients to be estimated by regression techniques from data already serially correlated.

Since it was derived specifically to cover the general case where fishing effort varies throughout an experiment, the second method, which yielded estimates of X as well as Z, did not necessitate any preliminary adjustment of raw data. In large degree, measurements of Z by both techniques proved mutually confirmatory.

TABLE 7.—*Unadjusted and adjusted numbers of marked pink shrimp recaptured during successive weeks of the Tortugas experiment, September–December 1961*

[Number liberated $(N_0) = 2,090$]

Week of experiment	Number recaptured	Distribution of males	Estimated total fishing effort [1]	Number recaptured per 1,000 hours' fishing effort	Log adjusted number recaptured
t_i	n		f	n'	$\ln n'$
		Percent	*Thousands of hours*		
0	47	55	2.11±0.23	22.3	3.105
1	68	51	2.80±0.52	24.3	3.190
2	44	54	3.98±0.30	11.1	2.407
3	15	47	2.82±0.30	5.3	1.670
4	14	61	0.92±0.11	15.2	2.721
5	184	55	3.78±0.20	48.7	3.886
6	37	42	4.04±0.43	9.2	2.219
7	24	67	5.83±0.47	4.1	1.411
8	6	67	10.07±0.62	0.6	−0.511
9	1	100	5.43±0.43	0.2	−1.609
10	0	----	6.98±0.73	0.0	----
11	0	----	8.92±0.65	0.0	----
12	3	33	9.14±0.48	0.3	−1.204

[1] 0.80 confidence intervals.

Subdivision of the Experiment

Preparatory to mortality estimation, plots of the adjusted Tortugas recapture data revealed a distinct but not unexpected discontinuity in the pattern of exploitation during the experiment (fig. 10). Prior to its fifth week, in which most members reached a size acknowledged to be the commercial minimum, the experimental population experienced a measurable amount of purposively selective fishing. Not until the beginning of the experiment's sixth week can it be presumed that recruitment to the "commercial" population was effectively complete. Most interest attaches to the experiment's second phase since estimates of fishing mortality between the points of complete recruitment to and virtual disappearance of
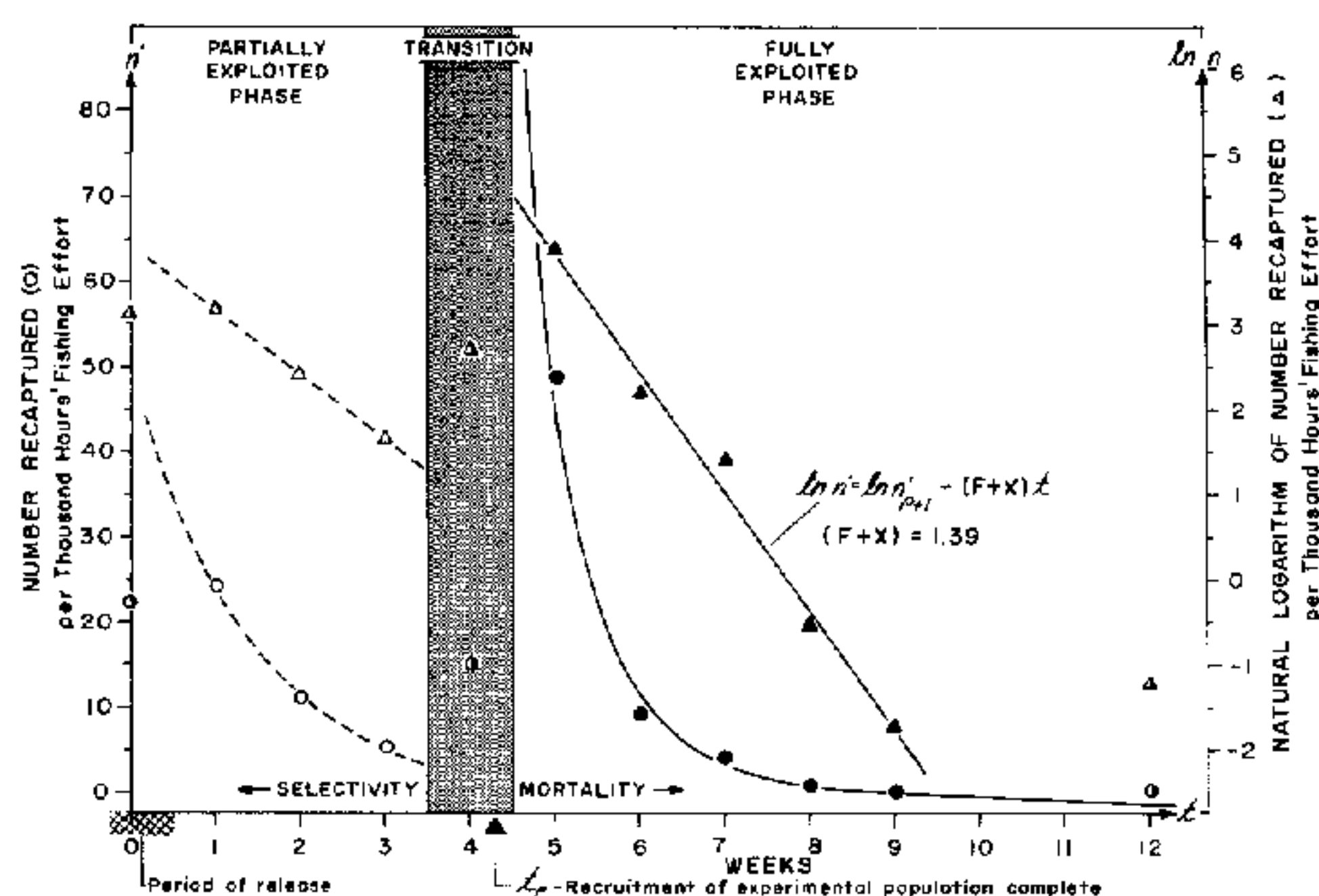
328

FIGURE 10.—Mortality of pink shrimp. Curves are fitted to numbers of marked shrimp recaptured during successive weeks of the Tortugas experiment (September–December 1961) and adjusted for nonuniform fishing effort. [Number liberated $(N_0) = 2,090$.]

the marked population from the fishery (i.e., from t_5 to t_{10}), and natural mortality just prior to and over the same period (i.e., from t_4 to t_{10}), are included among the major objectives of this study.

The experiment may therefore be conveniently subdivided into two phases arbitrarily separated by a brief (1-week) interval of transition. They are: (1) A period in population development when the fishery exercised moderate selectivity—the partially exploited phase, which was characterized by varying degrees of purposive as well as gear selectivity; and (2) a period of nonselectivity—the fully exploited phase, during which every population member was vulnerable to all operating causes of mortality.

Total Mortality During Partially Exploited Phase

Proceeding from theorem (1), which, upon transformation to logarithmic form, becomes linear in $\ln N_t$ and t, Beverton and Holt (1957, pp. 185–191) give in terms of the recaptures themselves a comparable expression intended for use with marked populations subjected to a uniform fishing (recapture) effort. Thus, making appropriate substitutions,

$$\frac{dn}{dt} = FN_t = FN_0 e^{-(F+X)t}$$

and, ultimately,

$$\ln n_2 = \ln n_1 - (F+X)\tau \qquad (2)$$

where $n_1, n_2, \ldots n_i$ refer to the number of marked individuals recaptured during the first, second, $\ldots i^{\text{th}}$ time interval t, respectively; $\tau = t_{i+1} - t_i$ $(= 1$ week$)$; F and X are the instantaneous coefficients of reduction of marks due, respectively, to fishing and to all causes other than fishing; and $(F+X) = Z$. It follows from expression (2) that a linear regression of the natural logarithms of successive numbers of recaptures on time gives estimates of $\ln n_1$ and Z.

Fitting a regression to the logarithms of Tortugas recaptures grouped by weeks and adjusted for nonuniform fishing effort (viz., $\ln n_1'$ through $\ln n_3'$, where the prime indicates an adjusted value) yielded an estimate of 0.76 for Z, the only parameter of interest during the experiment's initial phase. Figure 10 shows that the regression enjoyed a good fit.

Obviously, a measurable amount of (selective) fishing effort contributed to the total mortality value so obtained, though by far the greater share of this value is presumed attributable to natural causes. Only a very minor part is believed due to the "other-loss" factors defined earlier. There is moreover, no statistical evidence of any differential vulnerability of sexes during the partially exploited phase. Despite the slower growth noted for males, the sex ratio of recaptures never departed significantly from that observed at the start of the experiment (table 7). In summary, a small amount of fishing activity during the experiment's first phase was sufficient to demonstrate an apparently high corresponding rate of natural mortality, which, as will be shown later, continued well into the second or fully exploited phase. Here it became associated with the relatively high rate of fishing mortality established at the moment recruitment was completed.

Mortality During Fully Exploited Phase

After plotting the logarithms of the adjusted numbers of shrimp recaptured during the first 5 weeks of the Tortugas experiment's fully exploited phase, and observing that they, too, all fell nearly in a straight line (fig. 10), computation of their linear regression on time [equation (2)] gave a first estimate of $Z = 1.39$ for the instantaneous coefficient of mark reduction due to all causes.

Attempts to subdivide the resulting Z into its fishing mortality and "other-loss" components

proved impractical, however, when recapture data adjusted for varying fishing effort were substituted in techniques implicitly designed for unadjusted data generated by a uniform effort. Inspection of the basic equations involved (Beverton and Holt, 1957, p. 190, equations 14.15 and 14.16) reveals that the soundness of F and X (or M) estimated therewith may be influenced not only by the size of N_0 (or any specified equivalent), but also by variation in the relative magnitude of the antilog of $\ln n_1$ (or its counterpart), where the latter value is derived by means analogous to equation (2). It will be recalled that initial treatment of the recapture data entailed their being grouped on a weekly basis, and then adjusted within each time unit for nonuniformity of fishing effort between units by a factor equal to the reciprocal of the quantity $(f_i \times 10^{-3})$, with f_i representing the overall effort in hours expended on the fishing grounds during the ith weekly interval (table 7). Subsequent difficulty stems from the arbitrary nature of the attenuation index, 10^{-3}, which must be selected so as to yield adjusted recapture values having an average order of magnitude moderately close to that of the unadjusted values.

Whereas analysis of recapture data so adjusted provides [through expression (2)] a good estimate of the total-loss coefficient $Z = (F+X)$, such subjective treatment imparts bias of unknown degree to the values for F and X when these are delineated by the equations mentioned above. This bias will be proportional to the value of n_1 as estimated by expression (2), and, accordingly, to the relative size of the adjustment index employed. The real problem, however, lies in not being able to specify satisfactorily the relationship between N_0 and the estimated initial value of the recapture time-series based upon adjusted data, as contrasted to that between N_0 and the corresponding value of the time-series involving unadjusted data.

Drawing support from the fundamental theorem stating that over a given time interval r, fishing mortality is proportional to fishing effort (or intensity), i.e., $F_r = c f_r$, Beverton and Holt (1957, p. 192) derive solely in terms of recapture and related effort values a useful equation which furnishes—independent of N_0—an estimate of the other-loss coefficient X, regarded herein for the reasons outlined earlier as a close approxima-

tion of M. This equation is given by

$$\frac{1}{\tau_r}\left[\ln\left(\frac{n_r f_{r+1}}{n_{r+1} f_r}\right)\right.$$

$$\left.+\ln\left\{\frac{(cf_r+X)(1-e^{-(cf_{r+1}+X)\tau_{r+1}})}{(cf_{r+1}+X)(1-e^{-(cf_r+X)\tau_r})}\right\}\right]$$

$$=cf_r+X \quad (3)$$

where τ signifies the width (in weekly units) of experimental time intervals r or $r+1$, n identifies the number of recaptures in the same intervals, and c denotes the average coefficient of proportionality relating fishing mortality to fishing effort, f_r.

Equation (3), accounting inherently for varying fishing effort, is linear in f_r and a logarithmic expression (left side) corresponding to the ratios in successive time intervals of the numerical abundance of marked individuals composing the experimental population. Accordingly, simple regression procedures involving at least two iterations lead to fairly good estimates of c and X, the slope and y-intercept, respectively. The latter value may be viewed as a measure of the average total-loss rate that would have prevailed during the experiment in the absence of any fishing activity.

Use of expression (3) assumes that bias introduced by the practical need to treat fishing effort as a discontinuous function of time is negligible. Its application to appropriate recapture data and corresponding values of effective fishing effort gave, after three iterations, estimates of $c=0.171$, $X=0.55$, and average $F=0.96$ for the fully exploited phase of the Tortugas experiment (fig. 11). Interestingly, the resulting value for $Z=(F+X)=1.51$ compared quite favorably with the preliminary value calculated earlier, viz, $Z=1.39$, differing on the order of but 9 percent. Relevant statistics are presented in table 8. Note here the incorporation of effort data slightly modified from those used earlier to obtain the preliminary estimate of Z. The decision to subject to analysis only those measurements of effort expended inside 20 fathoms was prompted by the observation that none of the 252 marked shrimp retrieved during the period of interest (table 8) was recaptured beyond this range. Such adjustment seemed necessary to minimized the likelihood of violating, in terms of the experimental population and that portion of the fishery's overall activity
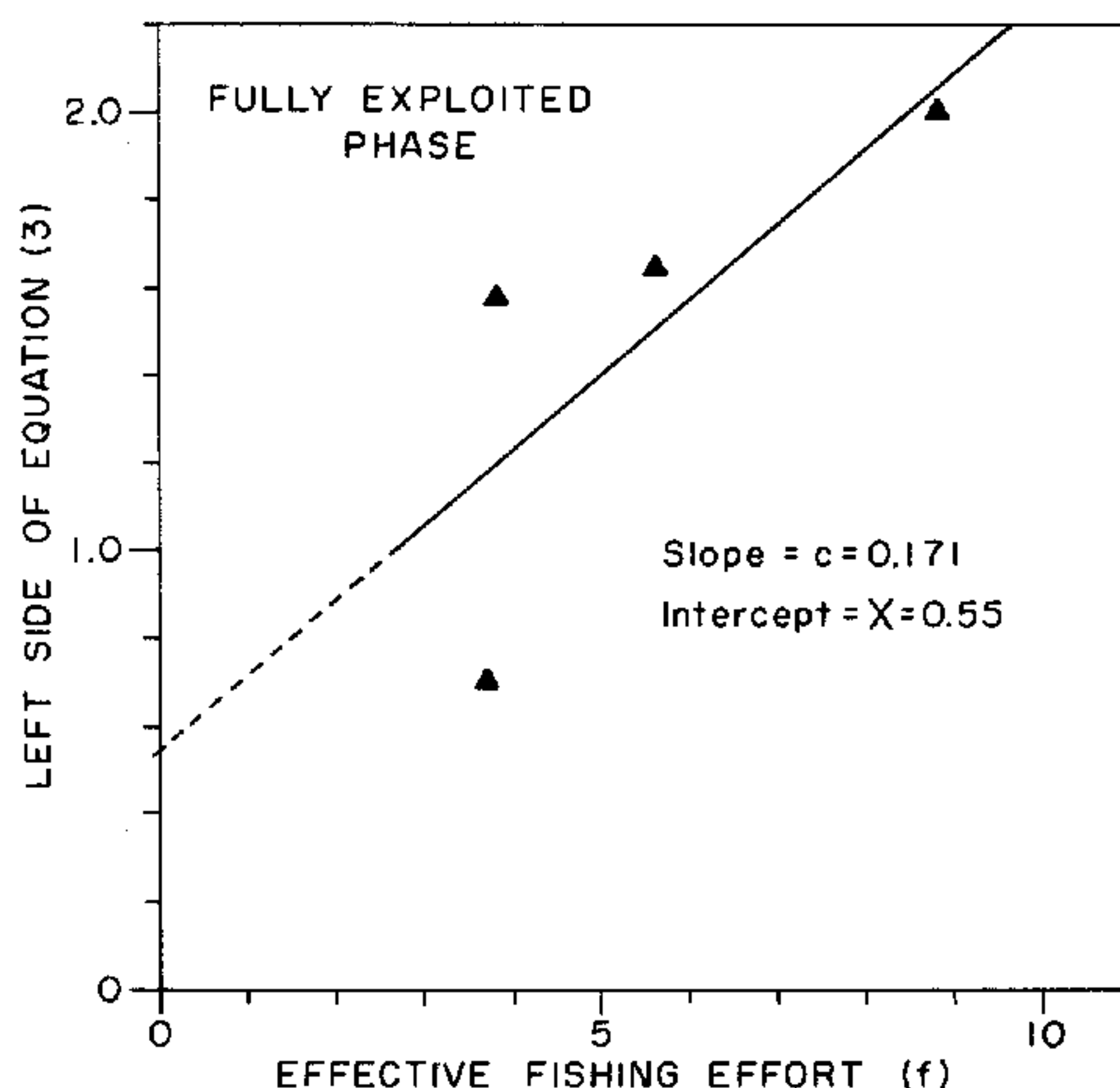

FIGURE 11.—Estimating the other-loss coefficient X using equation (3) of text. [Refer to table 8 for description of data and associated statistics.]

directly associated with it both spatially and temporally, the functional relationship between fishing mortality and fishing effort (or intensity) stated above.

Transformation of estimated F and X to corresponding weekly rates of reduction in marks resulted in values of 0.62 for that due to fishing, and 0.42 for that due to all other causes (see Ricker, 1958, p. 25, for discussion of relationships). These results, while indicative of greater mortality pressure on parent shrimp populations than had

TABLE 8.—*Statistics employed to estimate with equation (3) of text the other-loss coefficient X for the fully exploited phase of the Tortugas experiment*

[Resulting F values are given in the last column; $c=0.171$]

Week of experiment t_i	Rank in time-series r	Width of experimental time interval	Number recaptured n	Estimated effective fishing effort [1] f	Left side of equation (3)	Estimated fishing mortality $F=cf$
		Weeks		*Thousands of hours*	*Ln units*	
5	1	1	184	3.78	1.583	0.65
6	2	1	37	3.68	0.725	0.63
7	3	1	24	5.60	1.642	0.96
8	4	1	6	8.76	1.996	1.50
9–10	5	2	1	11.73		2.01

[1] Treated here as synonymous with *fishing intensity* which, in broader geographical application than is here necessary, is explicitly defined as fishing effort per unit area; data represent only that amount of effort expended on the Tortugas fishing grounds inside the 20-fathom contour (re table 2).

been widely speculated, are not unreasonable when one considers the species' high reproductive potential, short life expectancy, gregarious habits, and, presumably, its sensitivity to environmental fluctuations. Such characteristics, as they control population development, are not atypical of Arthropoda in general.

Returning to the matter of discontinuity in temporal distribution of recaptures during the Tortugas experiment (table 7, fig. 10), observe now that its further reconciliation is possible. The value obtained for X, 0.55, which is henceforth assumed for the reasons noted earlier to have been practically all due to natural causes, is readily contained in the total-loss coefficients estimated for both partially and fully exploited phases, viz, 0.76 and 1.51, respectively. If natural mortality is presumed to have been effectively constant through the transition period, then the difference in residuals (fishing mortalities, $F=0.21$ versus $F=0.96$) may be immediately attributed to cessation of selective fishing accompanied by an abrupt rise in fishing rate upon completion of recruitment. It appears that had the low rate of recapture established during the partially exploited phase continued, subsequent computations would also have led to an estimate for X (hence M) comparable to that determined from existing data for the fully exploited phase.

That the instantaneous rates of mortality do not remain constant over extended periods of time but diminish with age is suggested by a small number of marked shrimp having been recaptured late in the experiment. Note in figure 10 that their corresponding logarithm fell far to the right of the line fitted to those of adjusted numbers of recaptures made earlier in the experiment.

In summary, the foregoing results are interpreted to reflect exclusively conditions in that age group of shrimp represented by the experimental population, and hence should only be applied with great caution in other fisheries, or to other age groups at different seasons. Every age group (as herein defined) is but one of a succession of groups that may overlap several seasons. Each is therefore likely to be subjected at every stage of development to different levels of exploitation as well as to changing ecological conditions, with the high expectation that mortality parameters will vary accordingly.

YIELD IN WEIGHT AS A FUNCTION OF AGE (SIZE) AT RECRUITMENT

To answer the fundamental question posed earlier, it remains now to express the interaction of population growth and mortality in terms of expected yield when age (or size) at recruitment is varied over a wide range of values. Thus, so that the commercial return from a particular age group (or, in general, all age groups combined) will be maximal, at what average age of shrimp, under the conditions of observed growth and mortality, should harvesting begin?

THEORETICAL POPULATION MODEL

A satisfactory answer may be provided through application of any one of several mathematical population models, or analogs, which have been developed to facilitate study of the dynamics of open, self-maintaining biological systems (e.g., Watt, 1956; Beverton and Holt, 1957; Ricker, 1958). Notwithstanding its possible shortcomings, all of which are thoroughly discussed at appropriate stages in its derivation, the simple model developed and applied by Beverton and Holt (1957, pp. 35–38 and 309–327) was chosen for the purposes of this study because it offered the most straightforward solution to a practical problem.

Deterministic in nature, i.e., growth and mortality are presumed effectively constant from recruitment onward to the end of the species fishable life span, the expression for the shrimp population's mean weekly biomass over this period is given by

$$\overline{P}_W' = Re^{-M\rho}W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK} (1-e^{-(F+M+nK)\lambda})$$

where F and M are, respectively, the coefficients of instantaneous fishing and natural mortality; W_∞, K, and t_0' are the growth parameters defined earlier; R represents the number of shrimp recruited weekly to the fished population; $t_{\rho'}$ is the age, corresponding to the minimum commercial size referred to above, at which recruitment is no longer influenced by selective fishing; $\lambda=t_\lambda-t_{\rho'}$ indicates the population's fishable life span (t_λ being the species mean life expectancy); and $\rho=t_{\rho'}-t_\rho$ designates an interval during which some recruitment occurs because of selective fishing but population decline is mainly attributable to natural causes (t_ρ indicating the age at

which shrimp become liable to selective capture but, generally speaking, have not yet attained commercial acceptability). In practice, for a given set of conditions, ρ is usually negligible and $t_{p'}$ and t_p may be considered equivalent. The remaining notation arises from the need, during the model's development, to expand the exponential term of the von Bertalanffy growth equation.

Thus, if we let $b=3$,

$$w_t = W_\infty (1 - e^{-K(t-t_0')})^b$$

may be algebraically transformed to

$$w_t = W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t-t_0')}$$

where the appropriate coefficients of the binomial expansion are

$$\Omega_0 = +1, \; \Omega_1 = -3, \; \Omega_2 = +3, \; \Omega_3 = -1$$

with n taking the values 0, 1, 2, and 3. Although earlier analysis of the weight-length relationship suggested that growth in pink shrimp is not truly isometric, use of the foregoing model assumes, for practical purposes, that it is. Actually, the minor effects of a departure from isometry should be taken into account by appropriately varying W_∞, but failure to do so here does not lessen the validity of later findings.

From the biomass equation just postulated, it follows that an expression for the mean weekly yield of the fished population may be represented by

$$Y_W = F\overline{P}_W'.$$

And since R, the recruitment, is the only one of the parameters describing $\overline{P}_W'$ that is not ordinarily amenable to measurement, further modification results in

$$\frac{Y_W}{R} = \frac{F\overline{P}_W'}{R} = Fe^{-M\rho} W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{p'}-t_0')}}{F+M+nK}$$
$$(1 - e^{-(F+M+nK)\lambda}) \quad (4)$$

hereinafter referred to as the expected yield in weight per recruit.

DETERMINATION OF YIELD MAXIMUMS

By varying $t_{p'}$, and hence ρ and λ, curves of yield as a function of age can be generated with equation (4) for fixed values of the remaining parameters. The process obviously entails prior establishment of some absolute minimum value for t_p, this value corresponding in subsequent analyses to a size below which all shrimp are not only commercially unacceptable, but also incompletely vulnerable to the gear in common use.

Yield Curve for Observed Parameter Values

We have, from the Tortugas experiment and other sources, the following values for the indicated parameters:

$$M = 0.55 \qquad t_0' = 0.68 \text{ week}$$
$$F = 0.96 \qquad t_\lambda = 83 \text{ weeks}$$
$$K = 0.07 \qquad t_s = 15 \text{ weeks }[7]$$
$$W_\infty = 42.0 \text{ g.}$$

Recall also that $\lambda = t_\lambda - t_{p'}$ and $\rho = t_{p'} - t_p$. Substituting these in equation (4) and solving it for each of not less than nine carefully spaced values of $t_{p'}$, the yield curve farthest to the left in figure 12 was obtained. It is immediately apparent from this figure that in a population whose development is governed by growth and natural mortality of the magnitude observed for the Tortugas pink shrimp population, peak biomass is attained somewhat before, rather than after, the average shrimp reaches a size equivalent to the present commercial minimum. Growth, although relatively high in contrast to that determined for a variety of species supporting other commercial fisheries, evidently cannot compensate (to man's economic advantage) for losses accruing to a high natural mortality. Nor is postponement of full-scale exploitation indicated unless reduced environmental effects can be expected to result in a markedly lower natural mortality. Under observed conditions, delaying exploitation until the shrimp reach a greater initial size would indeed result in a negligible gain in yields of so-called premium shrimp, but only at the expense of a significant reduction in the total yield of all sizes.

Yield Curves Theorizing Lower Levels of Natural Mortality

Of the parameter estimates obtained in this study, by far the firmer and at the same time the least subject to wide temporal variation are those

---

[7] Age roughly corresponding to the minimum commercial size of 70 headless-count.
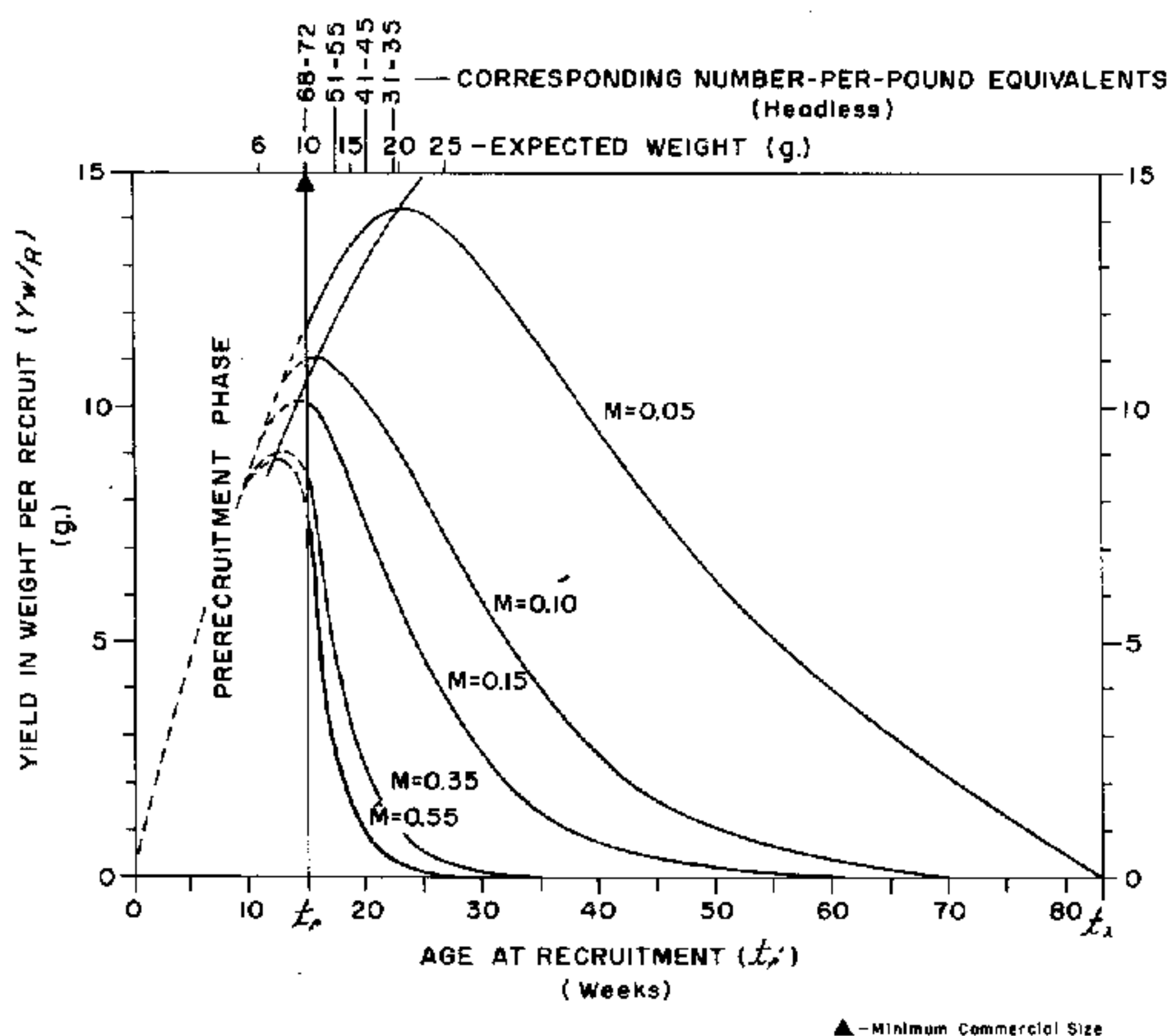
Figure 12.—Yield in weight per recruit against age at recruitment for different levels of natural mortality (M) in a population of pink shrimp. [$F=0$; 96, $K=0.07$; $W_\infty=42.0$ g.; ∧ indicates an observed as contrasted to a hypothetical value.]

describing growth. In contrast, greater variation would be expected for natural mortality since it may be readily conceived as the more sensitive to and hence the more likely of the density-dependent parameters to reflect even the most subtle of environmental vagaries. In other words the potentialities for growth in the individual are largely predetermined within rather narrow limits by the characteristics of the species; those for natural mortality, which are enhanced through great prolificness, largely by the environment.

With this in mind, additional curves were generated in like manner for four hypothetical and successively lower values of the natural mortality coefficient (fig. 12). These illustrate very clearly what happens when, with respect to some economic standard t_p, natural mortality becomes increasingly compatible with growth. For any magnitude of exploitation (F), maximum yields will always occur at higher levels and at more advanced recruitment ages as natural mortality establishes itself at lower and lower levels. Under the growth restrictions imposed here, postponing initiation of exploitation would not be justified unless the observed natural mortality rate were on the order of 0.10 or less. It may be argued now that even if the observed value for M (0.55) constituted a gross overestimate of the true natural

mortality, the associated error would have had to be rather large before the general conclusion just reached could be viewed with suspicion. The present example also shows that with a natural mortality of 0.05 (which is untenably low for shrimp), the highest yield is obtained when age at recruitment is increased to about 23 weeks, this corresponding to a shrimp size of roughly 31–35, headless-count. Dashed portions to the left of t_p arbitrarily designate the likely order and shape of the yield curves for that part of the hypothetical population not yet possessing economic worth.

Effects of Variation in Rates of Growth and Exploitation

To illustrate how changes in the critical factors of growth and fishing mortality influence the yield curve's shape and the position of its maximum point, curves for selected (hypothetical) parameter values are compared with those derived above for observed values. If yield is described as a function of age at recruitment for varying rates of growth (fig. 13A), it will be noted that the effect of a higher rate of growth than that observed is an increase in amplitude of the yield curve and a shift in its maximum point to the left, with whatever recruitment size is designated as the standard minimum remaining the same as before. In other words, every shrimp reaches the smallest acceptable size at an earlier age. Conversely, at a given level of natural mortality, a lower rate of growth tends to decrease curve amplitude and move the point of maximum yield to the right, the minimum marketable size again remaining fixed but being attained at a later age.

Exercising care to judge each new set of conditions on its own merits, it appears that increased rates of growth such as postulated in figure 13A would still not be sufficient to justify any advance of recruitment age where a high natural mortality prevails. At a low mortality level, an advance of recruitment age is indicated only when concurrent growth is also of a low order. Hence, for a fixed natural mortality, successively higher rates of growth would merely dictate a retrogression in recruitment age (but not size) if maximum yield is to be achieved. This relationship implies no change in minimum acceptable size at recruitment but, instead, as in the observed situation where low growth rate complements high natural mortality, a greater overall yield by the age group involved during its fishable life span.

By comparison, changes in the level of fishing may be expected to produce only relatively minor differences in both the position and height of yield curve maximums (fig. 13B). The revelation that the magnitude of fishing (F) is actually of little concern when deciding at what age or size to begin harvesting a resource in order to achieve maximum yields should not create the impression that fishing mortality has no significance at all. Although maximum utilization of a domestic shrimp resource is the issue under discussion here, the fact remains that resource maintenance is still the overriding objective of shrimp research. As pointed out earlier, the matter of recruitment age or size is at this point largely one of economics. Yet to be answered is the question of how much (in contrast to what size) shrimp may be harvested and still have sufficient residual to maintain the resource at the highest level consistent with projected environmental conditions. In effect, rather than inquiring as to the optimum $t_{\rho'}$, we should perhaps be asking: What is the optimum F?

Employing commercial fishery statistics, a prior analysis of the Tortugas pink shrimp stock gave rise to speculation that a decline in production over the period 1956–59 was attributable more to poor utilization of supplies than to too intensive fishing and hence improper maintenance of the stock (Kutkuhn, 1962). The observation was made that increasingly heavy exploitation of new recruits, as they enter the fishing grounds and before their average growth rate reaches a maximum, appeared to have systematically reduced annual biomass. Although this conclusion seems to be in conflict with the findings of the present study, it must be stressed that the earlier analysis was necessarily cursory due to certain data inadequacies and that it attempted to generalize over a long period of time and a variety of conditions. In contrast, the results reported here represent a well-organized effort to acquire the information needed to answer specifically the question posed. They are therefore quite explicit where the others were not, and, accordingly, merit much greater attention and could even be put to interim use.

The present findings do not, however, constitute the final solution to the stated question. As did those of the first analysis, they only reflect the accumulation of more and better data, and merely serve as one of several anticipated stepping stones toward an unassailable objective.
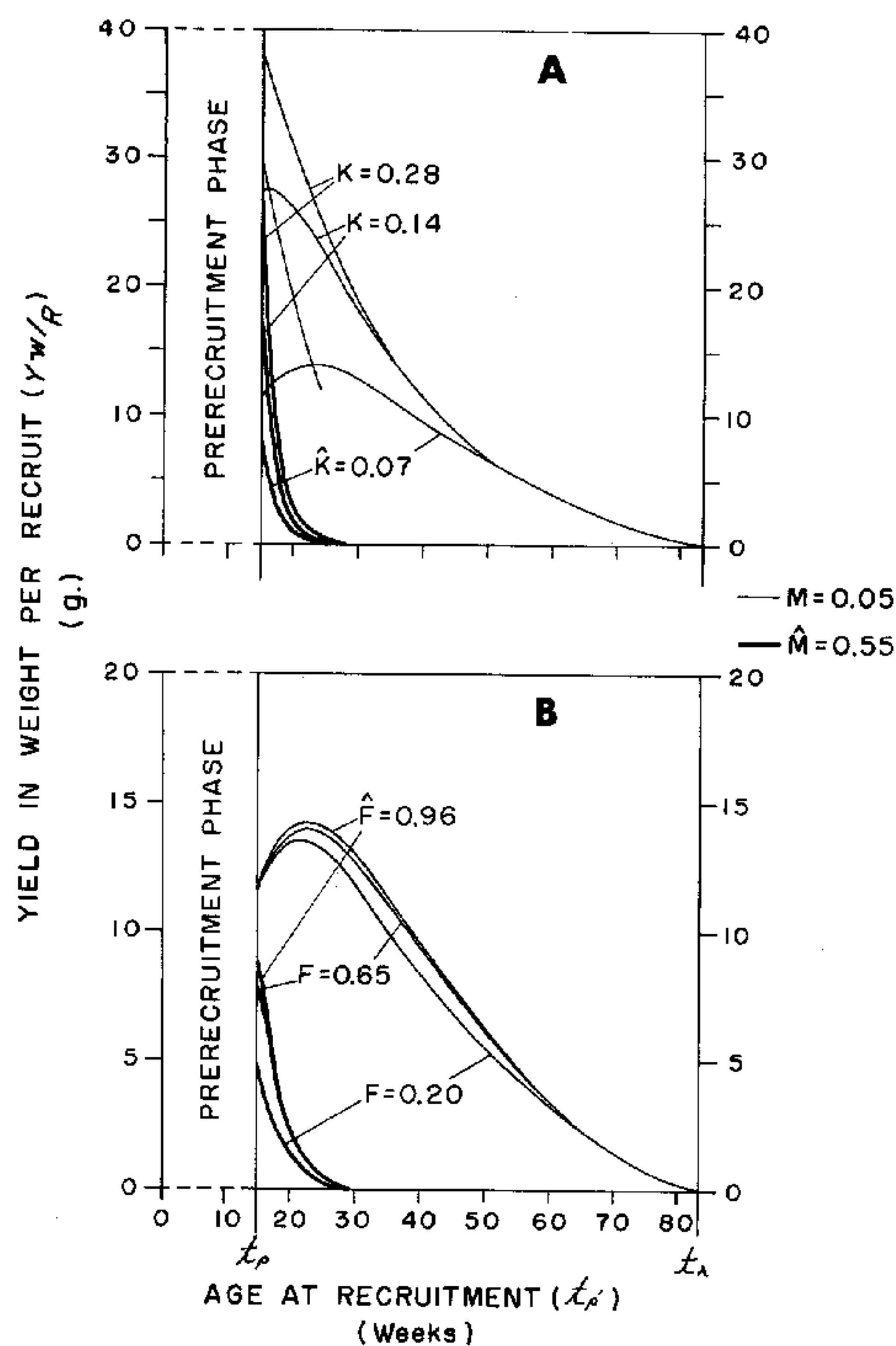

FIGURE 13.—Yield in weight per recruit against age at recruitment for observed and hypothetical levels of growth (K), fishing mortality (F), and natural mortality (M) in a population of pink shrimp. [In plate A, $F = 0.96$, $W_\infty = 42.0$ g., and the ordinate through $t_\rho = 15$ weeks refers, in terms of corresponding shrimp size, only to the curves for $K = 0.07$; in plate B, $K = 0.07$ and $W_\infty = 42.0$ g.; ▲ indicates an observed value.]

YIELD IN VALUE AS A FUNCTION OF AGE (SIZE) AT RECRUITMENT

Perhaps more meaningful to the entrepreneur is an indication of the size at which harvesting should commence so that total shrimp production will enjoy highest possible value. Necessitated by consumer demands, a well-known characteristic of the Gulf coast shrimp industry is the gradation of ex-vessel price according to the size of shrimp landed and sold. Knowledge of the price-size relationship may be used to advantage in determining where, in different growth and mortality

situations, the curve of yield value on recruitment age reaches a maximum.

VALUE IN RELATION TO SIZE

For the purposes of this study, particular attention was given the price structure for pink shrimp landed at Key West, Fla., during the Tortugas experiment, September to December 1961 (table 9). A plot of mean price on whole-weight equivalents for each of 11 size (headless-count) categories suggested that price could be treated as a logarithmic function of weight (fig. 14). The empirical relationship proved to be satisfactorily described by an equation of the form

$$p = a + b \ln [\ln w], \qquad w \lessdot 10$$

where p signifies the price per pound, w is the corresponding weight on an individual-shrimp basis, and a and b denote constants. Note that the expression has been rendered discontinuous at a shrimp weight of slightly more than 10 g., which corresponds to the minimum commercial size of 70 headless-count recognized earlier, and which commanded the lowest price then in effect (fig. 14). Dealers accepting them paid the prevailing minimum rate (30 cents per pound) for all smaller shrimp.

Having established a reasonably acceptable expression for the basic relationship between market price and individual shrimp weight, it was then possible to develop one relating the latter variable to corresponding shrimp value (fig. 14).

Data generated in the process served the needs of subsequent analyses.

VALUE AS A FUNCTION OF TIME

Since shrimp value increases predictably with weight, a corollary is that it behaves similarly with respect to time. Thus, simple transformation of weight to value units results in a temporal distribution of points which may be empirically defined by the growth equation employed in a previous section. By treating the Tortugas experimental data (table 4) accordingly, estimates of the constants in the regression of value on time were computed. The counterparts of W_∞ and K, respectively, $V_\infty = 4.8$ cents approximated the shrimp's maximum attainable value, and $K_v = 0.08$ represented an index of the rate of value decrease; t_0' remained fixed at 0.68 week, the value employed above in the description of growth in weight. When fitted to the experimental observations, the resulting expression for shrimp weight in terms of value as a function of time yielded a curve over the range of values 0.5 to 5.0 cents (per shrimp) closely comparable to that given by the corresponding expression for growth in weight.

DETERMINATION OF YIELD-IN-VALUE MAXIMUMS

After appropriate substitutions were made for the above growth-in-value constants, solution of equation (4) for various recruitment ages $(t_\rho,)$ at each of four levels of natural mortality (M) permitted construction of the desired yield-in-value

TABLE 9.—*Weekly ex-vessel prices paid for pink shrimp landed at Key West, Fla., 1961*

[Values are in cents per pound for headless shrimp graded by sample (box) count] [1]

Week ending	Size category (Number per pound—headless)										
	68–72	61–67	56–60	51–55	46–50	41–45	36–40	31–35	26–30	21–25	15–20
Sept. 16	32	40	41	50	51	57	59	64	69	74	79
23	31	36	41	46	51	56	61	66	71	76	81
30	27	31	41	46	51	56	61	66	71	76	81
Oct. 7	28	34	41	46	51	56	61	66	71	76	81
14	28	34	41	46	51	56	61	66	71	76	81
21	23	29	36	41	46	51	54	61	66	71	76
28	23	29	36	41	46	51	56	61	66	71	76
Nov. 4	26	32	39	44	49	54	59	64	69	74	79
11	29	35	42	47	51	56	61	65	70	75	80
18	29	35	42	47	51	56	61	65	70	75	80
25	32	38	45	50	54	58	62	67	72	77	82
Dec. 2	32	38	45	50	54	58	62	67	72	77	82
9	32	38	45	50	54	58	62	67	72	77	82
16	32	38	45	50	54	58	62	67	72	77	82
23	32	38	45	50	54	58	62	67	72	77	82
30	34	40	47	52	56	60	64	69	74	79	84
Mean	29.4	35.3	42.0	47.3	51.5	56.2	60.5	65.5	70.5	75.5	80.5
Whole-weight equivalents (g.)	10.5	11.4	12.6	13.8	15.3	17.0	19.2	22.1	26.1	32.5	41.7

[1] Source: Market News Service, Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service.
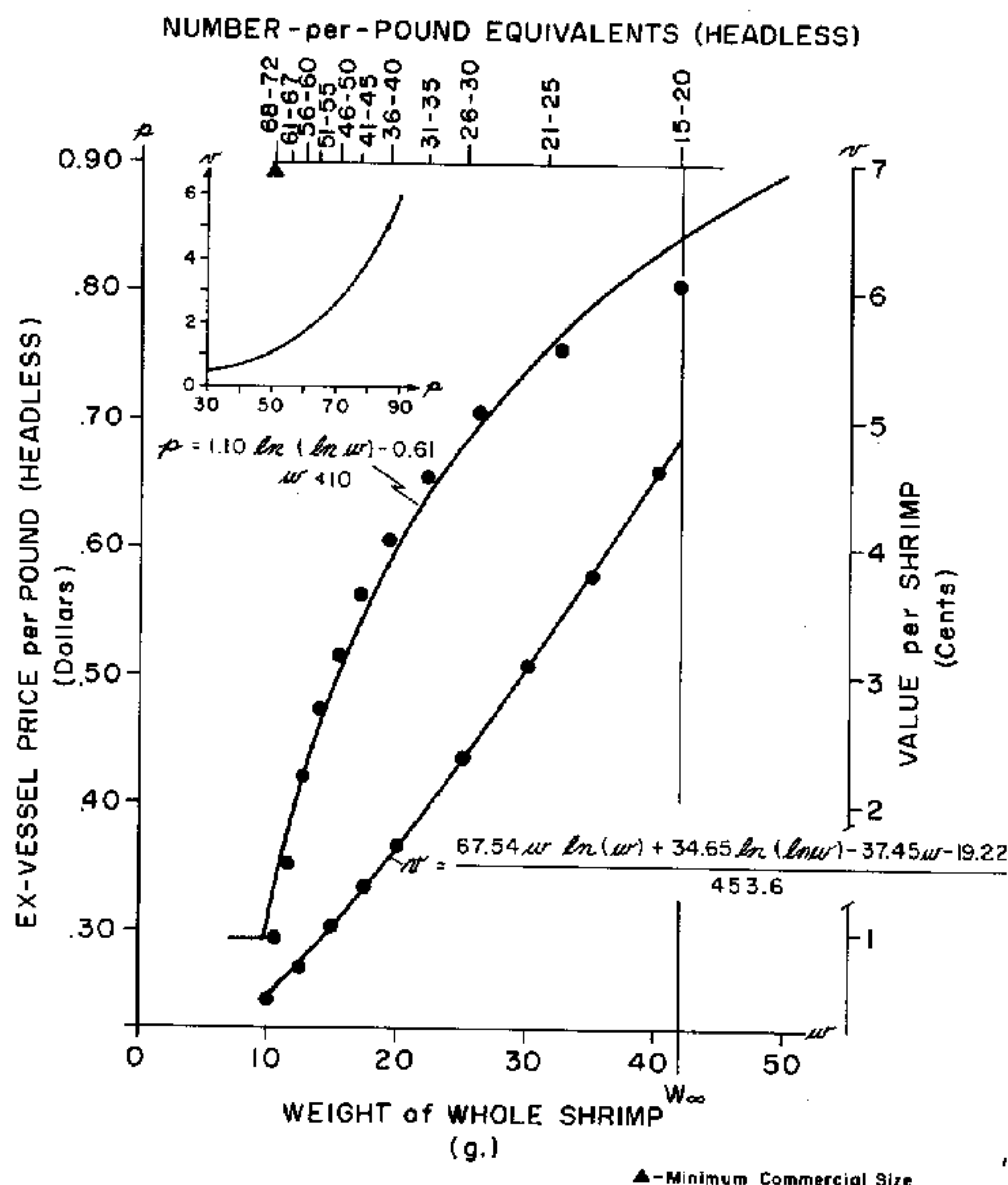
FIGURE 14.—Ex-vessel price (p) against weight (w) of pink shrimp landed at Key West, Fla., during September–December 1961. Also shown are the expression for converting price to value (v) on an individual-shrimp basis, and the resulting plot of value as a function of shrimp weight. In the upper left-hand corner, the value per shrimp in cents is graphed as a function of price per pound in the same units.
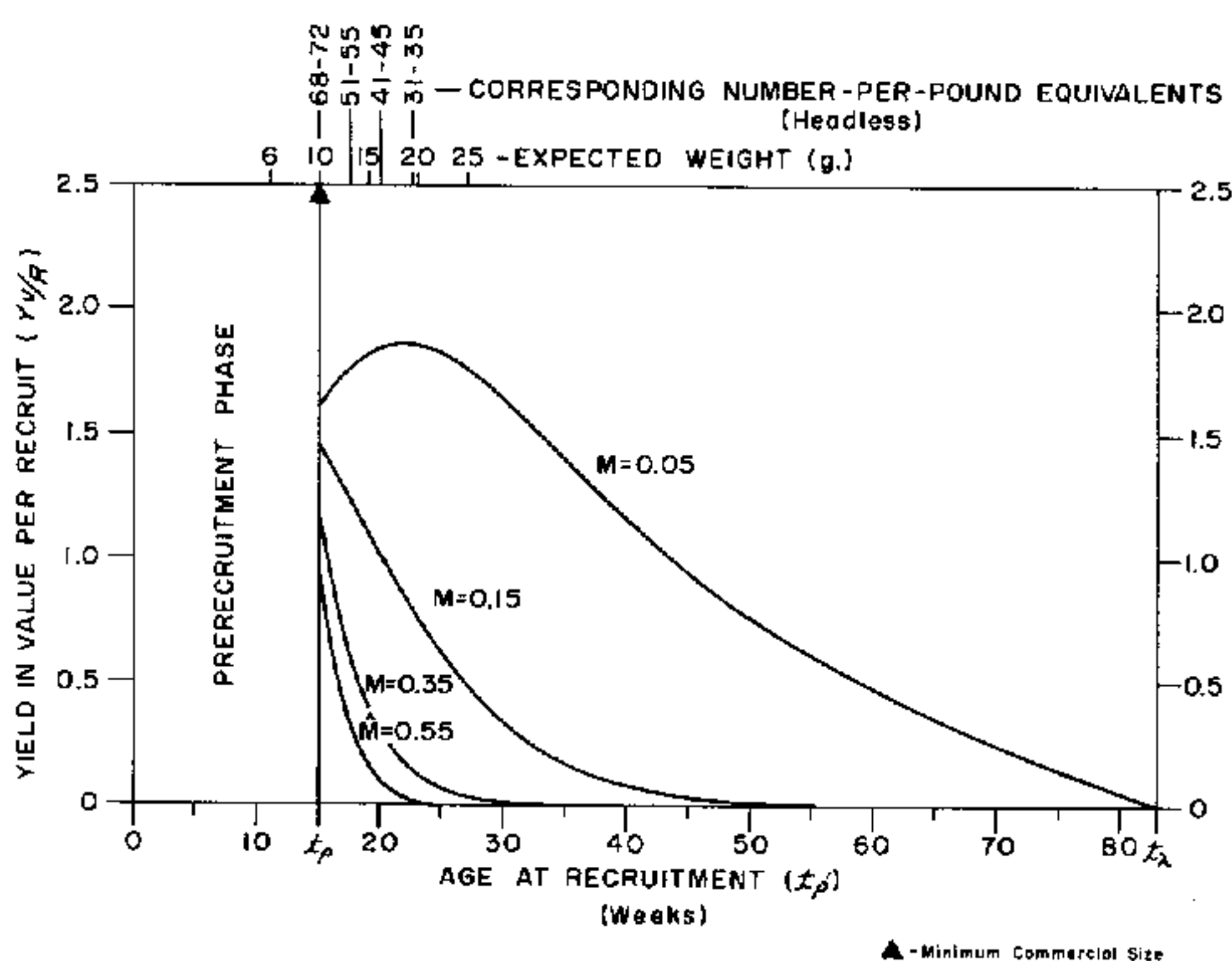

FIGURE 15.—Yield in value per recruit against age at recruitment for different levels of natural mortality in a population of pink shrimp. [$F = 0.96$; $K_v = 0.08$; $V_\infty = 4.8$ cents (per shrimp); ▲ indicates an observed as contrasted to a hypothetical value.]

curves (fig. 15). Upon comparing these with the yield-in-weight curves shown in figure 12, the most noticeable (though not necessarily significant) difference is seen in the relative positions of their maximum points. Unless natural mortality is extremely low, highest economic yield from a given age group during its fishable life span clearly occurs when exploitation begins as soon as the average shrimp attains commercial acceptance. In all but those circumstances where extraordinarily low natural mortality operates, no advancement of the recruitment age is indicated. This implies, of course, that the relationship between price and size holds relatively static.

Of interest is the general observation that, in situations where postponement of exploitation may be in order, maximum economic yield can be expected at a recruitment age (or size) slightly lower than that suggested for maximum biological yield. Figures 12 and 15 for $M = 0.05$ illustrate this very nicely. Note that the yield-in-weight curve (fig. 12) reaches its highest point at a recruitment size of about 31–35 count (headless), whereas the yield-in-value maximum occurs roughly at a headless-count somewhere between 36 and 40 (fig. 15). This difference is of appreciable biological magnitude and can be largely attributed to the somewhat higher rate of growth in terms of value ($K_v = 0.08$ versus $K = 0.07$). To reiterate, at levels of natural mortality known to be well within the range of expectation, the total yield of a given age group during its fishable life span will be maximal only when fishing begins at the minimum marketable size. Postponement to a larger initial size would engender economic loss.

SUMMARY

Measures of growth and mortality in a population of pink shrimp obtained simultaneously by the mark-recapture technique permitted critical examination of the interrelationship of these parameters in assessing present utilization of the resource.

Of 2,090 carefully graded, precommercial-size shrimp injected with blue dye and released in late September (1961) at a point on the periphery of the well-known Tortugas (Florida) fishing grounds, 443 (21 percent) were returned during the ensuing 3 months. Recapture (commercial fishing) effort was closely surveyed throughout this experiment

U.S. FISH AND WILDLIFE SERVICE

and then used to remove the effects of its uneven distribution from subsequent mortality estimates. Results of an earlier mark-recapture experiment performed with the same species but in an adjacent area and for a different purpose corroborated growth-parameter estimates from the Tortugas experiment.

After the various metric relationships used to convert length to weight units were documented, the von Bertalanffy growth function was fitted to the mean weights (sexes combined) of marked shrimp recaptured during successive, equal-width time intervals characterizing each experiment. The more meticulously executed Tortugas experiment yielded for the function's parameters the values: $W_\infty = 42.0$ g.; $K = 0.071$; and $t'_0 = 0.68$ week. Weekly growth in weight during the rectilinear phase of the observed growth pattern averaged 1.5 g., which corresponded to a length increment of about 3.4 mm. In terms of commercial count size, the average experimental shrimp required 12 weeks to increase in size from 123 to 37 headless-count. Minimum commercial size (70 headless-count) was reached approximately 4½ weeks after the experiment began, and at an estimated age of 15 weeks. The life expectancy of the pink shrimp was assumed on the basis of other studies to be about 83 weeks.

The Tortugas experiment had to be subdivided into partially exploited and fully exploited phases before fishing and natural mortality could be calculated. Rates of total mark-loss during both phases were estimated by regression techniques from recapture data grouped by weeks and adjusted for nonuniform fishing effort. Separation of the value obtained for the fully exploited phase into its fishing and natural mortality components, F and M respectively, proved impractical, however, when attempts were made to apply mathematical procedures designed specifically to accommodate unadjusted recapture data generated by a constant fishing effort. Difficulty arose from an inability to evaluate satisfactorily the absolute size of the experimental population at the start of its fully exploited phase. Subsequent measurement of F and M by a procedure independent of the initial size of the marked population's second phase, and inherently accounting for varying fishing effort throughout, yielded estimates of 0.96 and 0.55 respectively. Their transformation to weekly

mortality rates gave the corresponding values 0.62 and 0.42. Notwithstanding statistical limitations, these observations draw attention to the fact that at least in some areas, certain age groups (or broods) of commercial shrimp may be subjected to rather rapid deterioration from artificial as well as natural causes.

After substituting therein observed and hypothetical values for the parameters of growth and mortality, a relatively simple yield equation was solved for each in a series of selected age-at-recruitment values. With 15 weeks (corresponding to a size of 70 headless-count) established as the absolute commercial minimum age and thereby serving as the point of departure, the resulting curves of yield on age at recruitment clearly showed that unless the expected level of natural mortality falls well below that observed, postponement of fishing until shrimp reach a greater initial age (or size) is not justified. Observed growth, although comparatively high, cannot offset concurrent losses due to the substantial natural mortality that seemingly prevails when shrimp availability is at a maximum. Delaying the start of harvesting would subsequently result in slightly greater catches of shrimp in the larger size categories, but only at the expense of an appreciably diminished overall catch.

Even more convincing were the results of a similar analysis in which weight and hence the growth function's parameters were expressed in terms of value. For any level of natural mortality (observing the restriction imposed by the absolute commercial minimum presently in effect), maximum yield in value is attained when fishing commences at a shrimp size perceptibly below that at which maximum yield in weight would be expected.

The questions tentatively answered by this study have far greater implications from an economic than from a biological standpoint. Still of great concern is the problem of resource maintenance. We are unquestionably in a better position to judge when, in the development of any age group, the harvesting of shrimp should begin so as to obtain maximum production therefrom. But it remains for us to evaluate that level of fishing which, for a given set of environmental conditions and for the shrimp resource as a whole, is most conducive to our ultimate objective: maximum equilibrium yield.

ACKNOWLEDGMENTS

LITERATURE CITED

BERTALANFFY, LUDWIG VON.
  1938. Untersuchungen über die Gesetzlichkeit des Wachstums. II. A quantitative theory of organic growth. Human Biology, vol. 10, No. 2, pp. 181–213.
  1957. Quantitative laws in metabolism and growth. Quarterly Review of Biology, vol. 32, No. 3, pp. 217–231.
BEVERTON, R[AYMOND], J. H., and S[IDNEY] J. HOLT.
  1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food (Great Britain), Fishery Investigations, series 2, vol. 19, 533 pp.
COSTELLO, THOMAS J
  1959. Marking shrimp with biological stains. Proceedings of the Gulf and Caribbean Fisheries Institute, Eleventh Annual Session, November 1958, pp. 1–6.
  1964. Field techniques for staining-recapture experiments with commercial shrimp. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 484, 13 pp.
COSTELLO, T[HOMAS] J., and DONALD M. ALLEN.
  1960. Notes on the migration and growth of pink shrimp (*Penaeus duorarum*). Proceedings of the Gulf and Caribbean Fisheries Institute, Twelfth Annual Session, November 1959, pp. 5–9.
  1961. Migrations, mortality, and growth of pink shrimp. *In* Galveston Biological Laboratory, fishery research for the year ending June 30, 1961, pp. 18–21. U.S. Fish and Wildlife Service, Circular 129.
CUMMINGS, WILLIAM C.
  1961. Maturation and spawning of the pink shrimp, *Penaeus duorarum* Burkenroad. Transactions of the American Fisheries Society, vol. 90, No. 4, pp. 462–468.
DAWSON, C. E.
  1957. Studies on the marking of commercial shrimp with biological stains. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 231, 24 pp.
DOBKIN, SHELDON.
  1961. Early developmental stages of pink shrimp *Penaeus duorarum* from Florida waters. U.S. Fish and Wildlife Service, Fishery Bulletin 190, vol. 61, pp. 321–349.
IDYLL, CLARENCE P.
  1957. The commercial shrimp industry of Florida. Florida State Board of Conservation and Marine Laboratory, University of Miami, Educational Series, No. 6, 30 pp.
INGLE, ROBERT M., BONNIE ELDRED, HAZEL JONES, and ROBERT F. HUTTON.
  1959. Preliminary analysis of Tortugas shrimp sampling data, 1957–58. Florida State Board of Conservation, Technical Series, No. 32, 45 pp.
IVERSEN, E. S., and C. P. IDYLL.
  1959. The Tortugas shrimp fishery: The fishing fleet and its method of operation. Florida State Board of Conservation and Marine Laboratory, University of Miami, Technical Series, No. 29, 35 pp.
KUTKUHN, JOSEPH H.
  1962. Gulf of Mexico commercial shrimp populations—trends and characteristics, 1956–59. U.S. Fish and Wildlife Service, Fishery Bulletin 212, vol. 62, pp. 343–402.
LINDNER, MILTON J., and WILLIAM W. ANDERSON.
  1956. Growth, migrations, spawning and size distribution of shrimp *Penaeus setiferus*. U.S. Fish and Wildlife Service, Fishery Bulletin 106, vol. 56, pp. 553–645.
MENZEL, R. WINSTON.
  1955. Marking of shrimp. Science, vol. 121, No. 3143, pp. 446.
RICKER, W. E.
  1958. Handbook of computations for biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin No. 119, 300 pp.
TOMLINSON, PATRICK K., and NORMAN J. ABRAMSON.
  1961. Fitting a von Bertalanffy growth curve by least squares. State of California, Department of Fish and Game, Fish Bulletin No. 116, 69 pp.
WATT, KENNETH E. F.
  1956. The choice and solution of mathematical models for predicting and maximizing the yield of a fishery. Journal of the Fisheries Research Board of Canada, vol. 13, No. 5, pp. 613–645.